Aspects of the behaviour of African giant pouched rats (*Cricetomys sp*. nov) which impacts seed dispersal of large-seeded tree species in a West African montane forest landscape.

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Abstract

The loss of megafaunal vertebrate dispersers in tropical forests is strongly associated with seed dispersal limitation of large-seeded species. In the Neotropics, large scatterhoarding rodents such as agoutis and acouchies (Dasyproctidae) have been shown to be substitute dispersers of large-seeded species. In Afrotropical forests, the African giant pouched rat (*Cricetomys spp*) has the potential to disperse large-seeded species through scatterhoarding behaviour, but little was known about its behaviour in the forest. In this study, I investigated the behaviour of *Cricetomys sp*. nov in a Nigerian montane forest—Ngel Nyaki Forest Reserve (NNFR). NNFR comprises of Continous forests, forest fragments and grasslands. The main objectives of my study were to determine: i) the distribution of *Cricetomys* in relation to habitat ii) the distribution *Cricetomys* in relation to large-seeded species iii) the perception of *Cricetomys*' predation risk in different microhabitats and iv) the foraging behaviour of *Cricetomys* in relation to seed traits, fruit abundance and seasonal aridity. Using both live and camera trapping methods, I found that *Cricetomys* is mostly restricted to the forest core, less abundant in the forest edges and forest fragments, and almost totally absent from grasslands of NNFR. Within the forest core, I found that the density of *Cricetomys* varied markedly among patches. Although there was no relationship between the actual density of *Cricetomys* and large-seeded tree species, I found a significant positive correlation between the density of *Cricetomys* burrows and the abundance of large-seeded species. In contrast to many predation risk studies of small mammals, a combination of 'giving up density' (GUD) and a spool-and-line methods used in the forest revealed that *Cricetomys* did not perceive microhabitats with dense understories as safer sites. Using the classic thread-tagging technique for seed removal experiments, I found that seed nutrient content (especially fat) rather than seed size has a significant effect on seed fate. Seeds with higher fat content were more prone to predation while seeds with higher fibre content had a slightly higher probability of being dispersed. The use of artificial seeds across the wet and dry seasons revealed that fruit abundance rather than seasonal aridity had a significant effect on the fate of seeds removed by *Cricetomys* in NNFR because the frequency of seed removal was only altered by the availability of background seeds. The findings from this study suggest that seed recruitment patterns of large-seeded species may vary in different patches of montane forests. They also suggest that an increase in the population of

Cricetomys may have negative impacts on nutrient-rich large-seeded speeded species, while nutrient-poor large-seeded species may potentially have higher chances of being dispersed by *Cricetomy*s. Overall, this study has shown that *Cricetomys* may have a significant effect in seed-recruitment patterns of tropical montane forests.

Chapter 1: Background, scatterhoarding, small mammals and seed dispersal

1.1 Introduction

Scatterhoarding, an animal behaviour that involves the storing of food items in single caches, often plays a vital role in seed dispersal (Vander Wall, 1990; Vander Wall, 2010). The contribution of rodents to seed dispersal processes through scatterhoarding is already relatively well understood in many geographic locales (Forget & Vander Wall, 2001). In the tropics, it is probably the major contribution rodents make to the dispersal of large-seeded tree species. However, very little is known about scatterhoarding behaviour in African rodents (Nyiramana et al., 2011). In this Chapter, I review the literature on scatterhoarding, scatterhoarding rodents in the tropics and scatterhoarding rodent species in Africa. Specifically, my review addresses how the behaviour of the African giant pouched rat (*Cricetomys sp*p), the most common scatterhoarder of large seeds at my study site, influences its effectiveness as a seed disperser through scatterhoarding.

In this chapter, I also outline the research questions I developed in my thesis. To understand the behaviour of African giant pouched rats as scatterhoarding rodents, I begin this literature review by examining the concept of food hoarding by animals in general.

1.2 Food hoarding

Hoarding of food for future consumption has been well studied in many avian and mammalian species (Vander Wall, 1990; Brodin, 2010). There are two major food hoarding strategies – scatterhoarding and larder-hoarding (Vander Wall, 1990) and there is a clear distinction between them. Larder-hoarding involves storage of food at a central site by animals that are able to defend their resources while scatter-hoarders hide single food items in different locations because they are less able to defend stored food resources (Brodin, 2010). However, the two behaviours are not mutually exclusive; e.g. a study by Clarke and Kramer (1994) of Eastern chipmunks

(*Tamias striatus*) found that younger adults scatter-hoarded food items while older and stronger dominant individuals, i.e. those able to defend their caches against scroungers, larder-hoarded food. Some examples of mammals that exhibit the larder hoarding behaviour includes shrews, pine squirrels, pikas and some large kangaroo rats while scatterhoaders may include agoutis, achouchies, and some ground squirrels (Smith & Reichman, 1984); this means no animal taxa is limited to either scatter/larder loarding. Conspecific competition has been argued to be an important factor in the evolution of scatterhoarding (Smith & Reichman, 1984). The ecosystem consequences of scatterhoarding and the fascinating variation of this behaviour in birds and mammals have generated considerable interest among ecologists in recent times (Brodin, 2010).

Although studies of scatterhoarding began as far back as 1790 (von Pernau, 1790), the term was first used by Morris in 1962 to describe the hoarding behaviour of the neotropical green acouchies (*Myopracta pratti*) in captivity (see Brodin, 2010). The green acouchy was observed to hoard single units of dog biscuits offered to it on an even spatial scale within its 2x3 m cage (Morris, 1962). Subsequently, Nico Tinbergan, the famous ethologist, also observed scatterhoarding behaviour by a fox (*Vulpes vulpes*) in 1965 (Brodin, 2010). The fox was detected hoarding single caches of eggs taken from a colony of black-headed gulls (*Larus ridibundus*).

Scatterhoarding is important for many species because it helps secure food in times of food shortage. By being able to control the supply of available food, scatterhoarding animals can survive periods of food scarcity; this has thus become an adaptive strategy (Vander Wall 1990). Spacing out food resources minimises the chances of losing stored food to conspecific scroungers or other predators (Brodin, 2010). Because scatterhoarding ensures a supply of food for the future, scatter-hoarders can invest more time in other activities like courtship and territorial display (Vander Wall, 1990). However, the factors that foster scatterhoarding behaviour among mammals that show both scatterhoarding and larder-hoarding behaviours are still relatively unknown but background food abundance, population

density of the mammals and the environment of the mammals are probably the most important underlying factors (Smith & Reichman, 1984, Brodin 2010)

1.2.1 **Ecology of tropical scatterhoarding rodents**

Rodents that exhibit scatterhoarding behaviour are referred to as scatterhoarding rodents (Forget & Vander Wall, 2001). They often hide seeds in shallow caches (> 5 cm), and when hidden seeds are not revisited, they may escape predation, germinate, and establish as seedlings. Scatterhoarding by rodents is thus important in the maintenance of tropical forest ecosystems (Jansen & Forget 2001). Before 1990, seed dispersal by rodents, especially in tropical areas, received little attention from scientists (Vander Wall, 1990; Schupp et al., 2010). However, over the past two and half decades, there has been a surge of studies in both the tropics and higher latitudes, on seed dispersal by rodents, leading to the identification of and many species from different families as scatter-hoarders in the tropics. Notable among them are species in the families: Dasyproctidae, Muridae, Sciuridae and Nesomyidae (Forget & Milleron, 1991; Asquith et al., 1999; Yasuda et al., 2000; Theimer, 2001; Jansen et al., 2002; Nyiramana et al., 2011; Aliyu et al., 2014; Sidhu & Datta, 2015). Apart from their scatterhoarding behaviour, most scatterhoarding rodents around the world are different in habitat choice, body shape and size (Forget & Vander Wall, 2001).

The body sizes of tropical scatterhoarding rodents are variable, ranging from <300 g in Murid rodents to >2 kg in Dasyproctid rodents (Wilson & Reeder, 2005). These body size variations are often related to their densities, home ranges and resource utilisation. For example, a comparative ecology of the red acouchy (*Myoprocta exilis*) with its larger competitor - the orange-rumped agouti (*Dasyprocta leporina*) in French Guiana (Dubost, 1988) illustrates this point. In the study, 23 social units of relatively small acouchy and only 10 of the larger agouti inhabited an area 4 km^2; which suggested that larger scatterhoarding rodents occurred at lower densities. Densities of scatterhoarding rodents are, however, variable across different habitats and geographic ranges. A study by Jorge and Peres (2005) in Brazil showed that the

density of red-rumped agoutis was higher in areas with abundant food resources. However, the overall mean density was 31 individuals /km^2, was is three times lower than what was observed in Barro Colorado Island of Panama but about four times higher than what was observed in Tikal, Guatemala (Cant, 1977; Wright et al., 1999). To meet their nutritional requirements and store enough food, larger scatterhoarding rodents forage within wider areas including seed-poor habitats (Jorge & Peres, 2005), leading to reduced densities in such habitats.

1.2.2 Scatterhoarding rodents and seed dispersal

Scatterhoarding behaviour in rodents potentially makes them important seed dispersers, and as such, they can be beneficial to many tree species. Before 1980, the impact of scatterhoarding behaviour on seed dispersal was largely unknown despite the description of the behaviour in tropical rodents (Morris, 1962; Smythe, 1978). However, from 1990 onwards, an increasing number of studies, have continued to elucidate the strength of mutual interactions between scatterhoarding rodents and plants species. Theimer (2005) noted that scatterhoarding rodents could act either as conditional mutualist-seed dispersers or antagonistic seed predators when there is a change in the environment, e.g. changes in the abundance of food or competitors. In contrast, Jansen et al. (2004), showed that scatterhoarding rodents often maintain a balance between seed dispersal and predation in both high crop and seed-lean years.

The three advantages of seed dispersal for plants as proposed by Howe and Smallwood (1982) are: i) escape from distance and density-dependent limitations to seed recruitment such as pathogen attack, susceptibility to predators and competition (Escape hypothesis); ii) Colonisation of suitable habitats, relatively far from parent plants (Colonisation hypothesis) and iii) Directed dispersal by non-random means to specific sites that offer disproportionately high probability for seedling recruitment and survival (Directed seed dispersal hypothesis). An example of the escape hypothesis has been demonstrated in a study by Jansen et al. (2012) where the probability of seed mortality was lowered by removal and dispersal of

seeds by agouties. Although evidence for the colonization hypothesis is relatively weak for animal-dispersed tree species compared to wind-dispersed tree species in the tropics (Jansen et al., 2008), it is still a valid advantage of dispersal for tropical tree species (Terborgh et al., 2002). Further evidence for the escape hypothesis as well as the directed seed dispersal hypothesis was shown by Hirsch et al. (2012b); in that study, agoutis were shown to disperse seeds away forest sites with a high density of the palm trees. These advantages can only be examined if the deposition sites and post dispersal seed fates are known (Wenny, 2001). Since the 1990s when thread tags were used to track seeds removed by rodents (see Forget, 1990), seed tracking technology has advanced to include the of use radio telemetry (Forget et al., 2005; Hirsch et al., 2012a). Such advances have enabled studies that continually demonstrate the importance of scatterhoarding rodents in seed dispersal; especially with respect to the escape hypothesis (Forget, 1990; Jansen et al., 2004; Jansen et al., 2012). Nonetheless, a few studies have supported the role of scatterhoarding in the colonisation and directed dispersal hypotheses (Briggs et al., 2009; Hirsch et al., 2012b).

Being secondary seed dispersers (i.e. dispersers that remove seeds already dispersed by other mechanisms, e. g. wind, gravity or other animals), scatterhoarding rodents may provide additional benefits to primarily dispersed seeds by increasing their dispersal distances or caching them in sites that are more favourable for germination (Vander Wall & Longland, 2004). Although scatterhoarding rodents frequently remove seeds dispersed by gravity, an increasing number of studies have shown that they also remove seeds that are regurgitated or defecated by other vertebrates (Wenny, 1999; Forget & Milleron, 1991; Feer & Forget, 2002; Dutton et al., 2014). Often such seeds are taken farther away from their parent plants to growth-suitable locations.

Tropical scatterhoarding rodents may play a significant role in the dispersal of large-seeded tree species that have no extant mutualist megafauna dispersers (Jansen et al., 2012). Many studies in the tropics have shown that larger scatterhoarding

rodents disperse large seeded species (Forget, 1990, 1996; Jansen et al., 2002). Jansen et al. (2012) for example, described in detail, the dispersal of the large seeds of the cocosoid palm (*Astrocaryum standleyanum*) by the Central American agouti (*Dasyprocta punctata*). Using radio telemetry to track seed movement, they found that more than one-third of the dispersed *A. standeleyanum* seeds were moved >100 m away from their original points. The seeds were moved across long distances because of the high pilfering rates among Central American agoutis (Jansen et al., 2012). Although large-seeded trees have previously been only associated with megafauna in terms of dispersal, it can now also be argued that scatterhoarding rodents may have coevolved with large-seeded species (Jansen et al., 2012). Interactions between scatterhoarding rodents and large-seeded plant species may have stabilised long ago in the evolutionary history of the plants; theoretically, plants should have evolved mechanisms to discourage scatterhoarding by rodents if it had a negative net effect (Jansen & Forget, 2001). Moreover, given the pervasiveness of scatterhoarding in rodents, there is a possibility that this behaviour has had a selective pressure on plants to produce suitable sized seeds for scatterhoarders, although this is yet to be shown (Dennis, 2003).

1.2.3 **Factors influencing scatterhoarding behaviour in rodents**

A variety of factors have been suggested to influence scatterhoarding behaviour in rodents (Theimer, 2005; Hulme, 2002; Wang & Chen, 2009). While many studies focus on the effect of seed traits (e.g. seed size, nutritional content and defensive mechanisms) or rodent dispersal behaviour (Forget et al., 1998; Jansen et al., 2002; Wang & Chen, 2009; Galetti et al., 2010; Wang et al., 2014; Yi et al., 2015), others have considered environmental effects like masting years, fruiting season and rodent densities (Forget et al., 2002; Jansen et al., 2004; Forget & Jansen, 2007; Li & Zhang, 2007; Liu, et al., 2013). The results of both approaches suggest that scatterhoarding behaviour in rodents may be influenced by a combination of many factors.

Most studies of seed dispersal by scatterhoarding rodents stress the importance of seed size in influencing dispersal behaviour (Galetti et al., 2010). With regard to the tropics, rodents in two genera: *Dasyprocta* and *Myoprocta* have been more extensively studied compared with other scatterhoarding rodents (Forget, 1996; Peres et al., 1997; Forget et al., 1998; Asquith et al., 1999; Jansen et al., 2002; Jansen et al., 2004; Forget & Jansen, 2007; Vander Wall, 2010; Jansen et al., 2012). The majority of the studies in the tropics indicate that seed size positively correlates with distances at which seeds are cached. For example, Jansen et al. (2004) found seed size to be positively correlated with dispersal distance. In their study, *Carapa procera* seeds, ranging in size from 3 to 60 g were used to investigate the effect of seed size on dispersal distance. Seeds that were >20 g were more likely to be dispersed >10 m away from their original points (Jansen et al., 2004). Similar results were reported by Galetti et al. 2010, with large seed size being a significant factor for longer dispersal distances by agoutis (*D. leporina*). Using multiple seed species, they found that larger seeds were often dispersed across greater distances than smaller seeds; however, within a single species, they found that larger seeds were not dispersed over longer distances.

Intra-annual and inter-annual variation in seed abundance may also affect scatterhoarding behaviour in rodents (Forget et al., 2002; Jansen et al., 2004). While many studies have demonstrated positive effects of high fruiting season on scatter hoarding behaviour, others have shown the opposite (see Forget et al., 2002). Consequently, Forget et al. (2002) developed a model for scatterhoarding within one fruiting season; the model predicts that more seeds will be scatter-hoarded as the fruiting season declines. The reduction in both diversity and abundance of available fruits/seeds causes the rodents to hoard more seeds. However, in high fruiting seasons, abundance of available seeds causes satiation and thus lower hoarding rates (Forget et al., 2002). Similarly, Aliyu (2014) showed that *Carapa oreophila* seeds are more likely to be hoarded by *Cricetomys sp*. during the declining

fruiting season. In contrast, however, Jansen et al. (2004) in the Neotropics, demonstrated that fewer seeds of *C. procera* were likely to be dispersed by acouchies in high crop years, but the few seeds that were dispersed in high crop years had higher probabilities of survival.

Another important factor that affects scatterhoarding in mammals is conspecific density of the scatterhoarders. Conflicting views about the advantages (i.e. seed dispersal and tree recruitment) of high densities of scatterhoarding rodents in seed hoarding currently exist. For example, Li and Zhang (2007) demonstrated that seed dispersal through scatterhoarding can increase when rodent densities are low, while seed predation can increase with higher rodent densities. Similarly, Asquith et al. (1997) reported that the abundance of scatter-hoarding rodents had a negative effect on seed dispersal as seed predation increased i.e. most of the removed seeds were predated rather than dispersed. Conversely, Jansen et al. (2012) suggest that high densities of rodents might increase seed dispersal by thieving scatterhoarding rodents because of competition for food resources. Continuous pilfering of caches and moving seeds to other locations by conspecific scatter-hoarders increases the distance of seeds from parent trees. On the other hand, the density of scatterhoarding rodents may have no significant effect on dispersal of large seeds; a study by Forget et al. (1998) showed that scatterhoarding rates of large seeds (*Licania platypus* and *Gustavia superba*) were the same regardless of the density of the Central American agouti (*D. punctata*).

1.2.4 **Habitats of tropical scatterhoarding rodents**

Ecologists have diverse hypotheses about the factors that inform habitat choice in rodents (Lambert et al., 2006). Many tropical forests rodents seem to prefer habitats that are typical of forest edge, characterised by dense forest understory, and an abundance of vines (Lambert et al., 2006). While it was previously thought that these habitats were preferred because they provided cover from predators, Lambert et al. (2006) demonstrated that these habitats were most likely preferred

because they provided higher amounts of food resources. Alternatively, some rodent species prefer open forests with fewer understory plants. An example is shown in a comparative study of the red acouchy (*Myoprocta exilis*) and the orange-rumped agouti (*D. leporina*) by Dubost (1988). Red acouchies preferred dense understory forest sites while the orange-rumped agouties preferred forests with a lower density of understory plants. Density distribution of scatterhoarding rodents is often driven by food resources, availability of burrows, and predation risk (Endries & Adler, 2005; Aliaga-Rossel et al., 2008).

Although populations of scatterhoarding rodents may show seasonal fluctuations in abundance, higher densities are regularly observed in sites that hold abundant food resource trees (Beck–King et al., 1999; Aliaga-Rossel et al., 2008) and where nutritious large-seeded species are often abundant. An example of scatterhoarding rodents' preference for habitats that hold abundant large-seeded species is illustrated in a study of the red-rumped agouti conducted by Jorge and Peres (2005) in the Amazon. The density of red-rumped agoutis was significantly higher in areas rich in Brazil nut (*Bertholletia excelsa*) trees than areas where the trees were rare. It was suggested that the red-rumped agoutis preferred these areas because Brazil nut seeds were large and nutritious. Similarly, Aliaga-Rossel et al. (2008) showed that the Central American agoutis (*D. punctata*) often have overlapping home ranges in areas with an abundance of large-seeded *Astrocaryum standleyanum* trees and safe refuges, which suggests high densities of agoutis in these areas.

While predation risk and abundance of safe refuges are important in habitat choice of scatterhoarding rodents, little attention has been given to studying how predation risk affects the behaviour of scatterhoarding rodents in the tropics (Endries & Adler, 2005). Although the densities of rodents can be estimated by the number of available burrows when the frequency of a burrow use is known (Beck–King et al., 1999), little is known about how the density of burrowing scatterhoarding rodents relates to their actual density depending on whether

solitary or social species. Because burrow digging is common among social rodents that share the costs and benefits of digging burrows, the abundance of burrows in a localised area may be positively related to a large family, and thus high rodent densities (Ebensperger & Blumstein, 2006). It has also been suggested that burrow density may be linked to predation risk as rodents tend to construct more burrows in areas where predators are sparse, and food abundance is high (Ebensperger & Blumstein, 2006). While it is apparent that the abundance of safe refuges and food determine the habitat choice of neotropical scatterhoarding rodents (Aliaga-Rossel et al., 2008), very little or nothing is known about the effect of safe refuges or burrows in determining the habitat choice of Afrotropical rodents.

1.2.5 **Scatterhoarding rodents in Africa**

Despite the high diversity of trees in Africa, little is known about scatterhoarding rodents and their contribution to seed dispersal in this region (Forget & Vander Wall, 2001). This is probably because there has been a lot more interest in studying seed dispersal by primates and birds, which are recognised as long-distance seed dispersers (Forget & Vander Wall, 2001), mostly diurnal and charismatic species. One of the earliest scatterhoarding records in Africa can be traced to a behavioural study of the African ground squirrel (*Xerus erythropus*) by Ewer (1965). A pair of the ground squirrels reared in captivity and fed with nuts and grains were observed to hoard some grains, which they eventually tried to locate and eat or hoard again. Another study on African squirrels by Emmons (1980) in Gabon pointed to some scatterhoarding potential in African rodents. The large ground squirrel (*Epixerus ebbii wilsoni*) was reported to scatter-hoard nuts of *Panda oleosa* in well-spaced caches. In South Africa, the South-west Cape endemic murid *Acomys subspinosus* has been known to scatterhoard nuts of Protea species belonging to the genus *Leucadendron* (Midgley et al., 2002; Midgley & Anderson, 2004). Because of its small body size (<0.02 g), this rodent is only able to scatterhoard small seeds over a few square meters. More recently, the African pouched rat (*Cricetomys spp*), a relatively large rodent (~ 1 kg) has been identified as a potentially important scatter-hoarder in Sub-Saharan Africa (SSA) (Nyiramana et al., 2011; Aliyu et al.,

2014; Seltzer et al., 2015). The locations of the few rodent scatterhoarding studies carried out in Africa are shown in Figure 1.1.

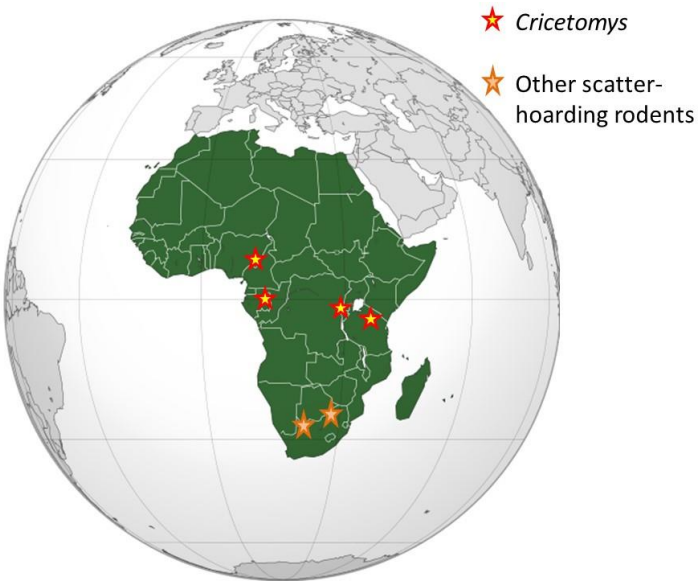

Figure 1.1: Locations (stars) of rodent scatterhoarding studies carried out in Africa. Stars were overlaid on map from Wikipedia (https://en.wikipedia.org/wiki/Africa).

1.3 African giant pouched rats *Cricetomys spp*

The African giant pouched rats *Cricetomys spp.* are among the large rodents of the tropical regions in Africa, although there are still conflicting views about the number of extant species in the genus (Ray & Duplantier, 2013). While a recent authoritative text broadly identifies four species of *Cricetomys* (*C. ansorgei, C. gambianus, C. emini* and *C. kivuensis*) in Africa (Musser & Carleton, 2005), another more recent investigation based on craniometrics and molecular evidence identified six distinct species (Olayemi et al., 2012). The study by Olayemi et al. (2012) re-grouped the species into *Cricetomys gambianus, Cricetomys ansorgei, Cricetomys emini* and three undescribed species classified as *Cricetomys sp*1, *Cricetomys sp*2 and *Cricetomys sp*3. However, because they lacked craniometric data for *C. kivuensis*, its existence could not be confirmed in that study. For ease of description, Ray and Duplantier (2013) separated the genus into two broad species – *C. gambianus* and *C. emini*. Following their classification, *C. emini* which has soft, dark brown pelage

with a pointed face is restricted to rainforests while *C. gambianus* has a pointed nose, blunt wide face with coarse greyish brown pelage is restricted to the edges of rainforests and savanna habitats (Ray & Duplantier, 2013). There are however no distinctive behavioural differences that support any of the *Cricetomys* classification systems.

African giant pouched rats (*Cricetomys sp*p) have been the focus of several studies (e.g. Ajayi, 1977; Verhagen et al., 2003; Weetjens et al., 2009, Nyiramana et al., 2011; Olayemi et al., 2012). However, few of these have related its general behaviour to its seed dispersal potential in tropical forests. While some studies have focused on its behaviour in captivity (Ajayi et al., 1978; Ewer, 1967), others have used it as a model system for detecting landmines (Verhagen et al., 2003), studying diseases such as pulmonary tuberculosis (Weetjens et al., 2009) and taxonomic investigations (Olayemi et al., 2012). Three recent studies (Nyiramana et al., 2011; Aliyu et al., 2014; Seltzer et al., 2015; Rosin & Poulsen, 2017) which span from western to eastern Africa, and from montane to lwland forests have demonstrated the seed dispersal potential of *Cricetomys* through scatterhoarding. Information on its ecology and general behaviour, however, which underpin its effectiveness as a seed disperser, are still lacking.

For example, while African pouched rats have been observed to utilise a variety of habitats ranging from forested areas to farmlands and human habitation (Ray & Duplantier, 2013; Ajayi, 1977), the basic determinants for their choice of habitats are still unknown. For example, sites which provide adequate food, good soil for burrows and less risk of predation may be preferred by *Cricetomys,* as has been observed for other scatterhoarding rodent taxa (e.g. Aliaga-Rossel et al., 2008).

The seed dispersal potential of *Cricetomys* has been reported in two montane forests (Nyiramana et al., 2011; Aliyu et al., 2014) and a lowland forest (Rosin & Poulsen, 2017) but the ecology of the species in these forests has not been studied. Following

the most recent seed dispersal studies involving *Cricetomys* in Ngel Nyaki forest Nigeria (Aliyu et al., 2014), additional studies into its ecology within this forest will further elucidate and clarify the role and significance of this species in seed dispersal.

Figure 1.2: An African giant pouched rat (*Cricetomys sp*. nov.) in Ngel Nyaki Forest Reserve. The long tail is partially covered by dead leaves.

1.4 Seed dispersal in the study area - Ngel Nyaki forest

Ngel Nyaki Forest Reserve (NNFR; 7.0876°N, 11.0534°E) is one of the most floristically diverse montane forests in Nigeria. This area contains several of Nigeria's endangered plant species, notable among which are the large forest tree species such as *Etandrophragma angolense, Lovoa trichilioides, Millettia conraui* and *Pouteria altissima* (Chapman & Chapman 2001). The forest also has a considerable amount of aboveground biomass, which indicates its importance in carbon sequestration (Adewoye *et al*., 2015). NNFR has however been negatively affected by severe grazing practices and annual bushfires that are usually ignited by Fulani pastoralists. These fires have led to the creation of wide open grasslands principally consisting of *Sporobolus pyramidalis* and *Hyperhnenia rufa* within the reserve (Barnes & Chapman, 2014).

Since 2006, seedlings have been planted in some areas of NNFR with the aim of restoring the forest (Hazel Chapman, pers. comm.). However, because forest restoration through seed dispersal processes involves little or no efforts, several studies have been carried out to understand seed dispersal systems in NNFR. Through these studies, dung beetles, birds, tantalus monkeys (*Chlorocebus tantalus tantalus*), putty-nosed monkeys (*Cercopithecus nictitans*), Nigeria-Cameroon chimpanzees (*P.t. ellioti*) and African giant pouched rats (*Cricetomys sp*. nov) have been documented as important dispersers of seeds in the Ngel Nyaki forest landscape (Agmen et al., 2010; Chapman et al., 2010; Aliyu et al., 2014; Dutton et al., 2014). Most of the animal seed dispersers in NNFR disperse only small to medium-sized seeds (< 25 mm in diameter), except for the chimpanzees and the African giant pouched rats that can potentially disperse larger seeds (>25 mm) (Chapman et al., 2010; Aliyu et al., 2014; Dutton et al., 2014). NNFR was an ideal place to study the contributions of *Cricetomys* to seed dispersal because most of the tree species and their associated seed dispersers/dispersal mechanisms are known.

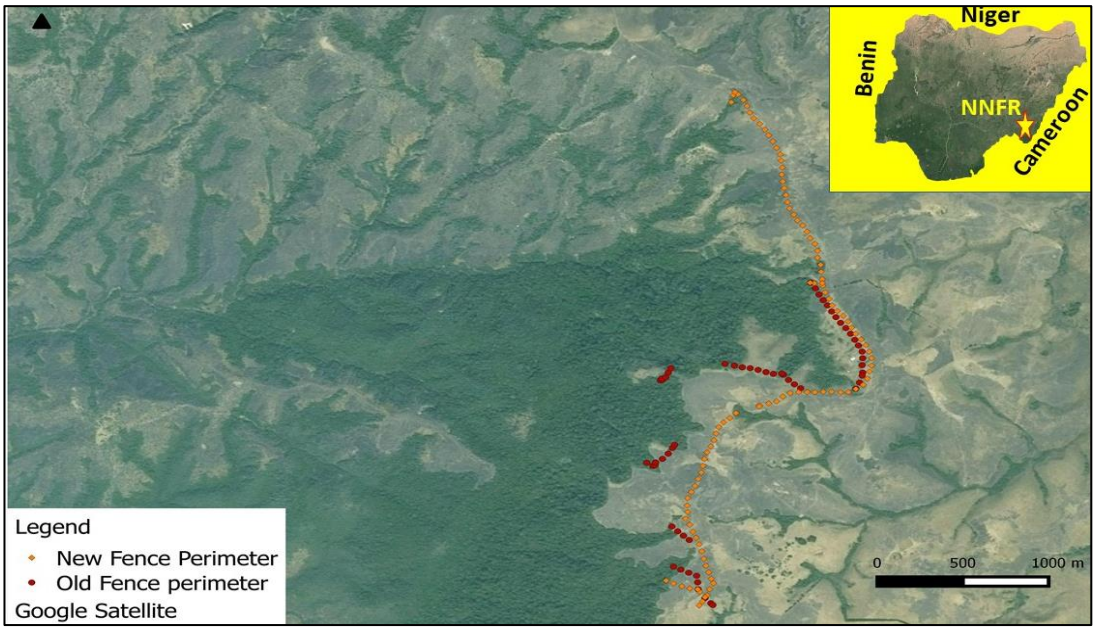

Figure 1.3: A satellite image of Ngel Nyaki Forest Reserve (NNFR) showing the largest continuous forests, surrounding grasslands and fenced areas which show conservation efforts of the Nigerian Montane Forest Project (NMFP). Map of Nigeria is inset.

There are strong indications that passive restoration strategies can be employed in Ngel Nyaki forest, as open habitats have shown a tendency to be recolonised by species from adjacent forests (Barnes & Chapman, 2014). African pouched rats, like other scatterhoarding rodents, may be very important in this process if they are not too selective of the seeds they eat.

Considering the global loss of forests (Hansen et al., 2010) and current forest conservation practices, results from this study may contribute to the global understanding forest recovery. In addition, the outcome of this study may provide useful insights as regards the future of forests holding little or no large vertebrate dispersers.

1.5 Aim and research questions

The overall aim of this study is to investigate aspects of the ecology of the African Giant Pouched Rat (*Cricetomys sp*. nov) in relation to its seed dispersal effectiveness in NNFR. The specific questions of this study include:

i. How are *Cricetomys* distributed in NNFR?
ii. Does the distribution of *Cricetomys* correlate with the spatial distribution of large-seeded trees in NNFR?
iii. Do microhabitat differences influence the perception of predation risk by *Cricetomys*?
iv. How do seed traits and fruiting season affect *Cricetomys* foraging behaviour?

The questions above are answered in the succeeding chapters of this thesis, and a final synthesis chapter is included at the end to highlight and discuss the main findings from the other chapters. In this thesis, I will mostly be referring to *Cricetomys sp*. nov as *Cricetomys* except in chapters 2 and 6 where I will be referring to it as *C. sp.* nov in order to compare it with other members of the genus.

1.6 References

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Chapter 2: Population dynamics and activity patterns of the African giant pouched rat *Cricetomys sp* nov. in Ngel Nyaki Forest Reserve, Nigeria

Abstract

The African giant pouched rat (*Cricetomys* spp) has the potential to be an important seed disperser of forest trees through its scatterhoarding behaviour. However, despite its widespread occurrence across the tropical African landscape, very little is known about its local distribution and activity in montane forests. In this study, I used two methods to estimate the seasonal density of *Cricetomys sp nov* in a Nigerian montane forest, live-trapping for Spatially Explicit Capture-Recapture (SECR) models, and camera trapping for a Random Encounter Model (REM). I hypothesised that: i) more *Cricetomys* will occur in the forest core and that the densities of the rat in different sites within the forest core will be the same. There will be no difference in frequencies of male and female rats, and iii) rats will be more active at the first half of most nights as is the case with many tropical rodents. The results supported the first hypothesis, showing that *Cricetomys* in Ngel Nyaki forest reserve was more common in the forest core than within forest fragments and grassland habitats. I found, however, that some forest patches supported higher densities of *Cricetomys* than others, and that males occurred at higher densities than females. I also observed that contrary to my third hypothesis, *Cricetomys* was more active during the early part of the night (19:00- 20:00 h) and before dawn (4:00 – 5:00 h). My results suggest that in montane forests, *Cricetomys* may occur at lower densities than in the lowlands and because of their density difference among forest patches, they may potentially vary in their influence on forest tree recruitment depending on the particular forest patch. The bimodal activity period of *Cricetomys* suggests that these rats may have a temporal strategy for predator avoidance or reduction in interspecific competition.

2.1 Introduction

A fundamental aspect of ecology is the distribution and abundance of species; this is because it provides an understanding of where a species occurs and what it interacts with (Andrewartha & Birch, 1954; Ehrlén & Morris, 2015). Although current distributions of organisms around the world are products of a long evolutionary history (Krebs, 2001), resource partitioning, body size and environmental limiting factors have also been proposed to be important in shaping species distribution patterns (Peterken & Game, 1984; Peters & Raelson, 1984; Guisan & Thuiller, 2005; Violle, Nemergut et al., 2011; Bothwell et al., 2015). Despite past and recent efforts to understand key factors that predict the distribution of species (Guisan & Thuiller, 2005), occurrence and distribution data for most tropical species are sparse (Elith et al., 2006).

Often, the distribution of animal species is related to the distribution of food resources or through interactions with other animal species. This is especially true for predator-prey distributions (Bernstein et al., 1999). For example, in Kenya, the eggs, larvae and cocoons of the silkmoth (*Anaphe panda*) are almost exclusively found on their host plants *Bridelia micrantha* (Mbahin et al., 2007). For such an interaction, the disappearance of the plant species might lead to the eventual loss of the associated animal species. Unfortunately, there are probably similar interactions that are yet to be documented in tropical forests (Bradshaw et al., 2009) and knowledge on the distribution and abundance of many flora or fauna species could be a significant step in the conservation of tropical forests. Additionally, because mammals often vulnerable and play an important role in passive conservation of forests in this anthropocenic era, it is important to give them priority when estimating abundance of organisms in forests.

2.1.1 Population density of forest mammals

The population density of a tropical forest mammal species is often closely related to its body size and trophic level (Damuth, 1981; Peters & Raelson, 1984; Robinson & Redford, 1986; Fa & Purvis, 1997; White et al., 2007). Typically, in forest

mammals, there is a negative relationship between body size and population density, with larger species occurring at lower densities (Damuth, 1987, 1991; Fa & Purvis, 1997; White et al., 2007). Body mass alone may account for up to 45% of the variation in population densities among Neotropical and Afrotropical forest mammals (Robinson & Redford, 1986; Fa & Purvis, 1997). Additionally, the density of mammals has been observed to decline as their trophic levels increases (Fa & Purvis, 1997). Fa & Purvis (1997), observed that the population densities of African forest mammal groups ranged from about 25-4500 individuals per km^2 for rodents, 2-175 individuals per km^2 for primates, 1-55 individuals per km^2 for ungulates, and 1-4 individuals per km^2 for carnivores. The above population densities assumes a little effect hunting

The relationship between body size and population density of mammals in tropical forests is often distorted by hunting (Peres & Dolman, 2000). Since most large-bodied mammals are the primary targets for hunters, the consequent reduction in their population densities often result in the increase of other groups of animals, e.g. small mammals (Effiom et al., 2014); this phenomenon is referred to as density compensation (MacArthur et al., 1972) or competitive release (Ruscoe et al.,2011). Evidence for density compensation comes from both Neotropical and Afrotropical forests. For example, Peres & Dolman (2000) showed that within primate communities in Neotropical forests, the population densities of medium-sized primates (1.5 - 4 kg) rapidly increased to counterbalance the decline of hunted populations of large-sized primates (> 4 kg). Similarly, Effiom et al. (2014) showed that with the reduction in densities of medium-large bodied primates (4-180 kg) in a Nigerian forest, there was a corresponding increase in the abundance of small mammals (e.g. porcupines and rock hyraxes).

2.1.2 **Demographics of small mammals**

Mammals that weigh < 5 kg are often categorised as small mammals (see Merritt, 2010) and mostly comprise of rodent species, which have a global distribution except for Antarctica (Patterson et al., 1989; Kelt et al., 1996; Fitzgibbon, 1997; Kay

& Hoekstra, 2008). Their small size, an adaptation for both predator avoidance and accessibility to food sources, enables small mammals to thrive in diverse habitats (Bourlière, 1975). Although they are largely omnivorous, many species of small mammals often occur in sympatry as a consequence of diet and habitat selection (Braithwaite et al., 1978; Dueser & Shuggart, 1979; Morris, 1996; Symes et al., 2013). The distribution of small mammals in different habitats is often influenced by a combination of factors that include predation risk (Barnum et al., 1992; Hughes et al., 1994; Abu Baker & Brown, 2010), interspecific competition (Falkenberg & Clarke, 1998; Perri & Randall, 1999) and availability of food and water (Getz, 1962; Miller & Getz, 1977; Schnurr et al., 2004). However, because most small mammals are generally prolific breeders (Batzli, 1999) living in environments with high risk of predation and finite resources, their population size often fluctuates remarkably at different periods; this is referred to as small mammals' population cycles (Krebs & Myers, 1974). Although population cycles in snowshoe hares (*Lepus americanus*) were hypothesised by early explorers and naturalists in Canada before the early 1920s, the phenomenon became well known among biologists after Elton's (1924) classic paper, which showed that population cycles are also common among other small mammals (Krebs, 1996).

Although many factors that can potentially explain population cycles in small mammals have been identified (Krebs & Myers, 1974; Batzli, 1992; Batzli et al., 1999; Oli & Dobson, 2001; Krebs, 2009; Cornulier et al., 2013), their relative importance and influence on population cycles are not well understood (Batzli, 1992; Cornulier et al., 2013). For simplicity, Krebs (1996) separated the hypotheses explaining population cycles of small mammals into five classes; these include i) food supply ii) predation iii) food supply and predation iv) qualitative changes in individuals and v) multiple factors including rainfaill. Food supply in an environment may be overexploited by a growing population, and then when food is scarce, the population may crash as a result of density-dependent mortality or emigration (Lack, 1954; Pitelka, 1957; Cole & Batzli, 1978; Klemola et al., 2000). Klemola et al. (2000) showed that excluding the predators of field voles (*Microtus agrestis*) and

sibling voles (*M. rossiaemeridionalis*) allowed their population to increase to a peak before crashing as a result of food shortages. Predators may affect the population cycles of small mammals by increasing their mortality rate via predation or by indirectly reducing the fitness of small mammals via their presence and abundance (Pech et al., 1992; Krebs, 1996, 2009; Korpimäki et al., 2002). By experimentally reducing the density of predators in western Finland, Korpikmäki et al. (2005) showed that small mammal populations increased rapidly. Apparently, the synergistic effect of food and predation is the strongest influence on population cycles of small mammals (Krebs et al., 1995; Korpimäki & Krebs, 1996; Klemola et al., 2000). However, Oli and Dobson (2001) argued that density-dependent changes in age at maturity and changes in juvenile survival are likely to be the leading cause of cyclic population changes in small mammals. The major factors affecting population cycles in small mammals may differ depending on a geographical scale. However, it is clear that multiple biotic and abiotic factors often interact to cause changes in population cycles (Batzli et al., 1999; Lima et al., 2003).

Although small mammals exhibit population fluctuations, habitat quality may play a role in stabilising population densities since low-quality habitats often serve as dispersal sinks for small mammals (Pulliam, 1988; Gundersen et al., 2001; Lin & Batzli, 2001). Small mammal habitats that are characterised by abundant food resources and herbaceous vegetation cover are often considered as high-quality habitats (Dunning et al., 1992; Lin & Batzli, 2001). Stenseth and Lidicker (1992) proposed that per capita emigration should be positively correlated with per capita population growth rate rather than population density in high-quality habitats. In an experiment to investigate the effects of habitat quality on population dynamics of prairie voles (*M. ochrogaster*) and meadow voles (*M. pennsylvanicus*), Lin & Batzli (2001) found that high-quality habitats (with abundant food and cover) were more likely to sustain high populations of small mammals than low-quality habitats.

Although there is little evidence for manipulation of juvenile sex ratios by adult small mammals, it is possible that maintaining a non-equal sex ratio could play an

important role in sustaining the population density of small mammals (Clutton-Brock et al., 1985; Clutton-Brock & Iason, 1986; Cockburn et al., 2002). Trivers and Willard (1973) proposed that among animal species, parental investment should alter offspring sex ratio by favouring the sex which has the greatest effect on the fitness of the species. If sex ratios are not balanced at adulthood, then a sex-structured population may continuously be observed in such a species. Even though a sex-structured population is expected to be prevalent in polygynous species (Cockburn et al., 2002), Komers and Brotherton (1997) suggested that monogamous mammals within a particular area are more likely to show a sex-structured population when females are solitary and occupy small, exclusive home ranges. However, an understanding of the population structure in small mammals may be confounded by the behavioural response of different sexes to the sampling methods. For example, Buskirk and Lindstedt (1989) found that male Mustelids (a family of small carnivorous mammals) are more likely to be trapped than female mustelids as a result of behavioural differences between the sexes.

2.1.3 **Methods for sampling small mammals**

Field surveys used in the estimation of small mammal population densities can generally be classified into three categories; non-trapping methods, removal trapping and non-removal trapping (Smith et al., 1975; De Bondi et al., 2010; Hoffmann et al., 2010). Because each category of field survey method has its advantages and disadvantages, a chosen survey method should be based on the species to be studied, length of study period and the secondary aims of the study (Smith et al., 1975; De Bondi et al., 2010). Non-trapping techniques may include direct sampling techniques e.g. line transect surveys (Chiarello, 2000; Smith et al., 1975) or indirect methods such as tracking boards, sand transects, dung counts, chew-track-cards, hair tubes and camera trap surveys (Smith et al., 1975; Hunt et al.,1987; Scotts & Craig, 1988; Baker et al., 2003; De Bondi et al., 2010; Hoffmann et al., 2010; Sweetapple & Nugent, 2011). More recently, camera traps have gained more popularity over other non-trapping survey methods because they can be operated for long periods of time under extreme weather conditions and used for

both diurnal and nocturnal mammals (Peterson & Thomas, 1998; González-Esteban et al., 2004; Vine et al., 2009). Also, camera traps can be used to sample multiple species at a time and do not place animals under physical stress, thereby having little or no effect on animal activity (Moruzzi et al., 2002; Kelly & Holub, 2008; De Bondi et al., 2010). Before the idea of estimating animal density through the 'Random Encounter Model' (REM) (Rowcliffe et al., 2008), animal density estimations through camera surveys were restricted to animals with individually identifiable markings (Rowcliffe & Carbone, 2008). The REM was based on the Ideal Gas Model which considers area (space), speed, density and total travel distance to predict the number of contacts for a certain particle (Rowcliffe et al., 2008). Assuming camera trap rates (photos captured over a given time) are analogous to the number of contacts of a particle, then animal density which is unknown can be derived from the other known variables (Rowcliffe et al., 2008). This method provides a relatively accurate estimate of the population density of animals that are not individually distinguishable (Rowcliffe et al., 2008; Rowcliffe et al., 2013).

Although trapping methods frequently involve stressing or killing the target species, they are relatively more advantageous in certain situations (Smith et al., 1975; Mills et al., 1995; Flowerdew et al., 2004; Wilson et al., 2007). For example, removal trapping methods may provide useful information (e.g. absolute population size, morphometrics and population growth rates) of small invasive mammals, which are often pests outside their native habitats (Wilson et al., 2007). Non-removal trapping methods are useful for marking animals and collecting samples for laboratory analyses, e.g. DNA or pathogenic analyses (Hoffmann et al., 2010). Despite the difficulty in small mammal surveys of using live-trapping methods, they are still preferred by ecologists because they provide detailed information about the target small mammal species on a finer scale. For example, individual movement distances, changes in body condition, preferred habitats and a relatively unbiased estimate of population density can be obtained using live-trapping methods (Otis et al.,1978; Pollock et al., 1990; Efford, 2004; Efford et al., 2004; Wilson et al., 2007; Efford & Fewster, 2013). Density estimates of small mammals in live-trapping

studies have been shown to be more reliable under the recently developed 'Spatially Explicit Capture-Recapture' (SECR) framework (Efford, 2004; Efford et al., 2004; Wilson et al., 2007). Because SECR estimates density without the need for calculating effective trap area, it can avoid biases resulting from the effects of home range sizes, the edge of the trapping grid and trap layout (Efford, 2004; Wilson et al., 2007; Efford & Fewster, 2013;). Given these advances in survey and analyses methods, it would be expected that the population dynamics of small mammals should be relatively well understood across the globe. Nevertheless, there is an apparent knowledge gap in population studies of small mammals in the tropics (Mares & Ernest, 1995).

2.1.4 **Population dynamics of small mammals in the tropics**

Due to a bias toward large mammal studies in tropical forests, the study of relatively small mammals in these habitats has received little attention (Mares & Ernest, 1995). Most studies of small mammals in the tropics are primarily concerned with their community structure and distribution in different forest habitats (Chiarello, 2000; Fitzgibbon et al., 1995; Goosem, 2000; Wijesinghe & Brooke, 2005; Umetsu & Pardini, 2007). Very few studies (e.g. Mares & Ernest, 1995) have attempted to quantify changes in populations of small mammals over time. Using a live-trapping method in a Brazilian gallery forest, Mares and Ernest (1995) showed that the population sizes of small mammals are low in the driest periods of the year. The paucity of small mammal studies is especially true in Africa, and this is surprising because African forests are facing diverse threats, which include hunting and logging (Malcolm & Ray, 2000). Understanding the dynamics and activity patterns of small mammal populations is critical for conservation of these forests because these small mammals have strong interactions with tree species via seed predation and dispersal and many are important prey for carnivores.

2.1.5 **Distribution of African giant pouched rats.**

Although African giant pouched rats (*Cricetomys* spp) have shown to interact with large-seeded tree species (Nyiramana et al., 2011; Aliyu, 2014; Aliyu et al., 2014;

Seltzer et al., 2015; Rosin & Poulsen, 2017), very little is known about their population and movement ecology in their native habitats. However, in Florida where *Cricetomys spp* being typically monogamous, have become invasive, the females hardly go beyond 100 m from their burrows while the males may exceed 200 m (Engeman et al., 2006). Following Olayemi et al. (2012), the species diversity of the genus *Cricetomy*s may also be reflected in variation in their behaviour, but little or nothing is known about the behaviour of the diverse species apart from two main species (*Cricetomys gambianus* and *Cricetomys emini*) recognised by Ray and Duplantier (2013). Additional knowledge on the morphology of these rats may be useful in determining their taxonomy (Olayemi et al., 2012).

Despite the known nocturnal behaviour of *Cricetomys*, little or nothing is known about the specific time at which these rodents are most active. This knowledge could shed light on its predator avoidance and interspecific competition strategies. African giant pouched rats have been shown to disperse seeds of montane tree species through their scatterhoarding behaviour (Aliyu et al., 2014; Nyiramana et al., 2011). One of these montane forests (Ngel Nyaki Forest Reserve—NNFR) is in Nigeria, and it provides habitat for some tree species on the International Union of Conservation Nations (IUCN) red list (Chapman & Chapman, 2001). Thus, understanding the ecology of the African giant pouched rat (*Cricetomys* sp. nov) is essential for the conservation of this, and other similar, montane forests where it occurs. As described in Chapter 1, the landscape of NNFR is basically composed of continuous forests, grasslands and forest fragments. In this study, I focused on the population dynamics and activity patterns of the African giant pouched rat (*Cricetomys* sp. nov; hereafter referred to as *Cricetomys*) in the different habitats of NNFR.

2.1.6 **Predictions**

To achieve the aim above, the following predictions were proposed:

i. Microhabitats with structures (e.g. burrows) that aid escape from predators would favour the presence of *Cricetomys*

ii. There is no difference in male and female *Cricetomys* morphometrics because they are monogamous

iii. *Cricetomys* in NNFR would predominantly occur in the forest habitat compared to other habitats since it is closely related to *Cricetomys emini* which prefers forested areas

iv. The density of *Cricetomys* would be even in the forest core areas because the forest cover is relatively even in the core

v. Male and female *Cricetomys* would occur at equal densities because they are monogamous

vi. The radius length of *Cricetomys* home range is < 100 m because home ranges are expected to be smaller in the rat's native habitats

vii. The peak activity period of *Cricetomys* would occur during the first half of the night as it the case with many nocturnal small mammals.

2.2 Methods

This study was carried out in NNFR (details about the study site are shown in the introductory chapter) between December 2015 and September 2017. Field surveys for *Cricetomys* density were carried out directly using live-traps and also using camera traps. I employed both methods because of their different advantages; while live-trapping provided the opportunity to handle, measure and mark trapped individuals (De Bondi et al., 2010), camera trapping provided the flexibility of non-invasive survey (Rowcliffe et al., 2008) of *Cricetomys* and other animals in the different habitat types in NNFR, i.e. forest core, forest edge, forest fragment and grassland habitats (see Figure 2.1).

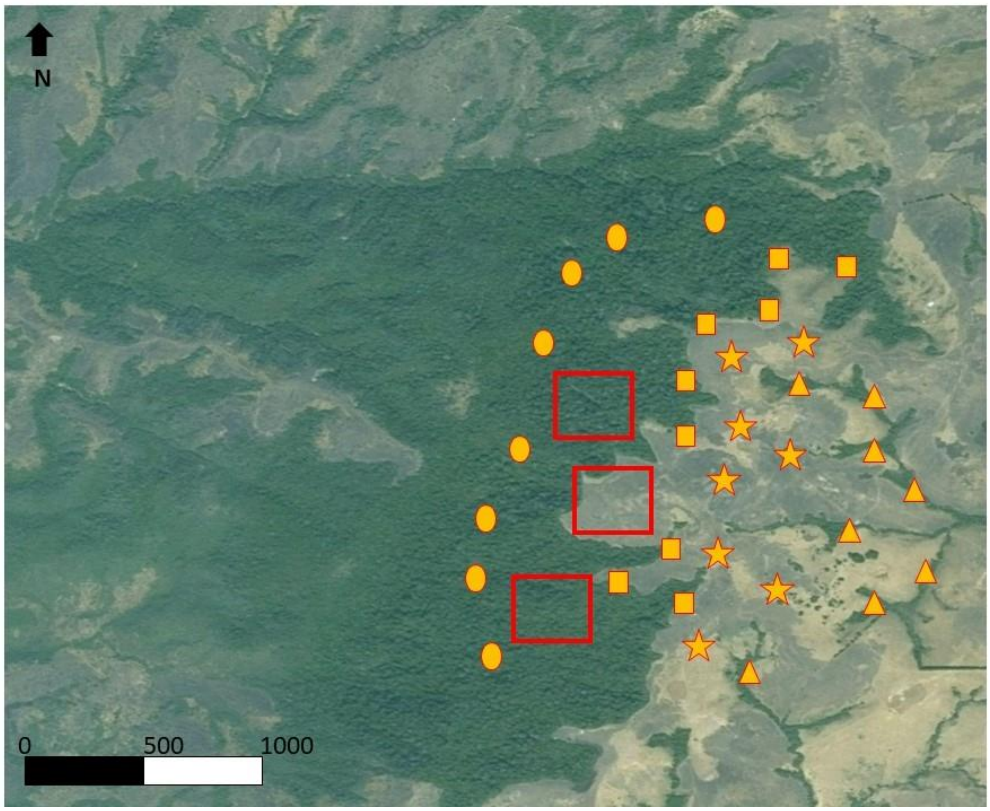

Figure 2.1: A google satellite image of the main continuous forest block of NNFR showing locations of live-trapping grids (large red boxes) and camera trapping sites (shapes filled with yellow; circles=forest core, squares = forest edge, triangles = forest fragments and stars = grasslands) in the present study.

2.2.1 **Live-trapping**

In this survey, a capture-mark-recapture (CMR) method (Krebs, 1999) was used to determine *Cricetomys* density in three different forest sites in NNFR; two in the forest core and one at the grassland-forest edge. The survey was carried out over five sessions in each site, with each session lasting five consecutive nights mostly in the dry season(Dry season—Mid November to March; Wet season—April to Early november. The five trapping sessions were carried out in December 2015, January 2016, April 2016, December 2016 and January 2018 to achieve a robust CMR design (Pollock, 1982). The robust design proposes that intense sampling should be carried out during several short windows of time (weeks in this study) that are separated by

longer intervals of time (months) during which, birth, death, immigration and emigration may occur (Amstrup et al., 2010). To ensure a sufficient sample size, I used 64 (Wilson et al., 2007) single catch cage traps (61x20.3x20.3cm; reproduced after Havahart® collapsible cage trap, Easy Technology Solutions Limited, New Zealand). Traps were arranged in an 8 x 8 grid (Efford & Fewster, 2013) and spaced 30 m apart. The trapping grids were at least 400 m apart to ensure independence, given that the known *Cricetomys* home range width is less than 200 m (Ray & Duplantier, 2014). Traps were baited with sweet potatoes (*Ipomea batatas*) (Joshua Thia pers. comm.) and peanut (*Arachis hypogaea*) cakes. The traps were checked every morning between 6:00 hours to 7:00 h and each captured rat was marked with a uniquely numbered set of metal ear tags (National band and tag company®, USA) on both ears in the first three sessions. Rats captured in the last two sessions were marked with uniquely numbered passive integrated transponder tags (Tierchip® sterile ISO-compliant microchip with implantation device ISO-Transponder 1.4 x 8.5 mm IG) in their subcutaneous dorsal region. For each trapped individual, sex, body length, weight and trap location were noted. Males with conspicuous scrotums and conspicuously lactating females were also noted. Re-trapped individuals in each session were noted and immediately set free to minimise stress for the rats. During the pilot experiment, I anaesthetised captured rats with Isofluorane (see the method in Ruscoe et al., 2011) but because the anaesthesia was difficult to administer, risky for the rats and offered no apparent advantage, rats were gently handled without any form of anaesthesia in the main experiment. All captured rats were released at their points of capture. At every trap point, micro-niche habitat characteristics including elevation, slope, percentage canopy cover, litter depth, number of dead logs and herb cover within in a 5 m radius, and proximity to the nearest water source, were recorded.

2.2.2 **Camera trapping**

Since the trapping grids in the live-trapping experiments above were too large to fit into the forest edge or forest fragment habitats of NNFR, I used camera traps (Bushnell® Trophy cam) to survey *Cricetomys* density within the four main habitats,

i.e. forest core, forest edge, forest fragment and grasslands. Eight camera traps were randomly placed in each of the habitats mentioned above such that the distance between any two cameras was at least 40 m so as to reduce the chances of having multiple cameras in a single home range. I carried out four different camera trapping sessions in this experiment; each session lasting ten days and camera locations were changed after each session. To reduce the chances of capturing an individual animal multiple times during one visit to a location, the cameras were set to capture one image of a moving animal per minute. Each photo from the camera trap data was visually inspected for species identification.

2.2.3 **Statistical analyses**

To determine microhabitat variables that influence the presence of *Cricetomys* in the live trapping experiment, I used a linear mixed effect model with a binomial error structure in R (R Core Team, 2017). *Cricetomys* were assumed to be present in only microhabitats where they were trapped and absent elsewhere; this was used as the response variable. The other microhabitat variables, i.e. elevation, slope, percentage canopy cover, litter depth, number of dead logs, cover of herbs and proximity to nearest water source, were set as the predictor variables, while the grid sites and trap locations were set as random variables. Using a backward elimination method and comparison of model AIC, the best model which had the lowest AIC was selected.

Student's t-test was used to compare morphometric measurements, i.e. head length, body length, tail length and body mass, between the male and the female *Cricetomys*. I used a Random Encounter Model (REM) to determine the density of rats from the camera trap data in the four main habitats. Camera traps that malfunctioned during the experiment were not included in the analyses. The REM model as described by Rowcliffe et al. (2008) is

$$D = \frac{y}{t}\frac{\pi}{vr(2+\theta)}$$

where D = *Cricetomys* density, y = number of photographs, t = period of camera trapping (hours), v = speed of movement (distance travelled per day, m/day), r = detection radius of camera (m), θ = detection zone of camera (radians) and π = 3.142. The only variable in the model that was difficult to obtain was "*v*", because there is very little information about the total distance that can be covered by *Cricetomys* in one night, thus I used 100 m as reported by Engeman et al. (2006).

Using Spatially Explicit Capture-Recapture (SECR) models in the 'secr' package (Efford, 2017) in R (R Core Team, 2017), the density of *Cricetomys* from the live-trapping experiment was determined from the *Cricetomys* capture histories and trap layout. SECR allows the use of models with varying CMR assumptions such as individual and temporal variation. Since rats were trapped singly, I used the maximum likelihood (ML) prediction in the models. Additionally, I included the habitat covariates, i.e. elevation, slope, percentage canopy cover, litter depth, number of dead logs, herbs and proximity to nearest water in the different models and then selected the best model as the model with the lowest AIC and AIC weight. Apart from density, I used the best SECR model to determine population size (N) and other spatial scale parameters, including mean distance between consecutive capture locations (dbar), the mean maximum distance moved (MMDM) and the root pool spatial variance (RPSV: a measure of animal movement used in the estimation of density). Although a home range size cannot be directly estimated from SECR analyses, a 95% and 50% probability of detection can be used as surrogates for home range (HR_{95}) and home range core area (HR_{50}) respectively (Ringler et al., 2014). Thus, I used the circular hazard distribution below (Ringler et al., 2014) to calculate the 95% and 50% probability area of *Cricetomys* detection.

$HR_{95} = \pi \times (3.6 \times \sigma)^2$

$HR_{50} = \pi \times (1 \times \sigma)^2$

Where σ is the realised spatial scale parameter representing home range width from SECR analyses output (see Wilson et al., 2007)

Using a Mann-Whitney U-test, I compared the SECR density estimates in the two forest sites. The grassland site was not used in the SECR analyses because a minimum of 10 capture event is needed. I also compared the SECR density of male and female *Cricetomys* using a Mann-Whitney U-test. The extent of *Cricetomys* movement was viewed in a histogram plot. Similarly, I used a frequency polygon to determine periods of activity for *Cricetomys*.

2.3 Results

My results showed that *Cricetomys* in NNFR frequently occurred in habitats that were extensively covered with forest trees. During the total of 4800 live-trap nights, 183 *Cricetomys* capture events were recorded; of which 100 were unique individuals (Table 2.1). Among the microhabitat variables measured, only the number of burrows that had a significant positive correlation with the presence of *Cricetomys* (Table 2.2); the probability of trapping a *Cricetomys* was higher in microhabitats with more burrows (Figure 2.2).

Table 2.1: Summary of *Cricetomys* live-trapping data in the three different sites in the present study

Habitat	**Male**	**Female**	**Total captures**	**Unique captures**	**Deaths**
Forest_site1	49	22	71	39	2
Forest_site1	76	29	105	55	1
Grassland_forestedge	5	2	7	6	0
Total	**130**	**53**	**183**	**100**	**3**

Table 2.2: Effect of habitat factors and number of burrows in predicting the probability of trapping *Cricetomys*. The best model: Capture/No-capture = Dead logs + Litter +Burrows, Family =Binomial, had an AIC value of 629.32 compared with the second-best model with an AIC value of 639.61

Parameter	Estimate	Standard error	z value	p value
Intercept	-2.462	0.835	-2.95	0.003**
Dead log	0.006	0.016	0.39	0.696
Litter	0.011	0.010	1.079	0.280
Burrows	0.221	0.091	2.431	0.015*

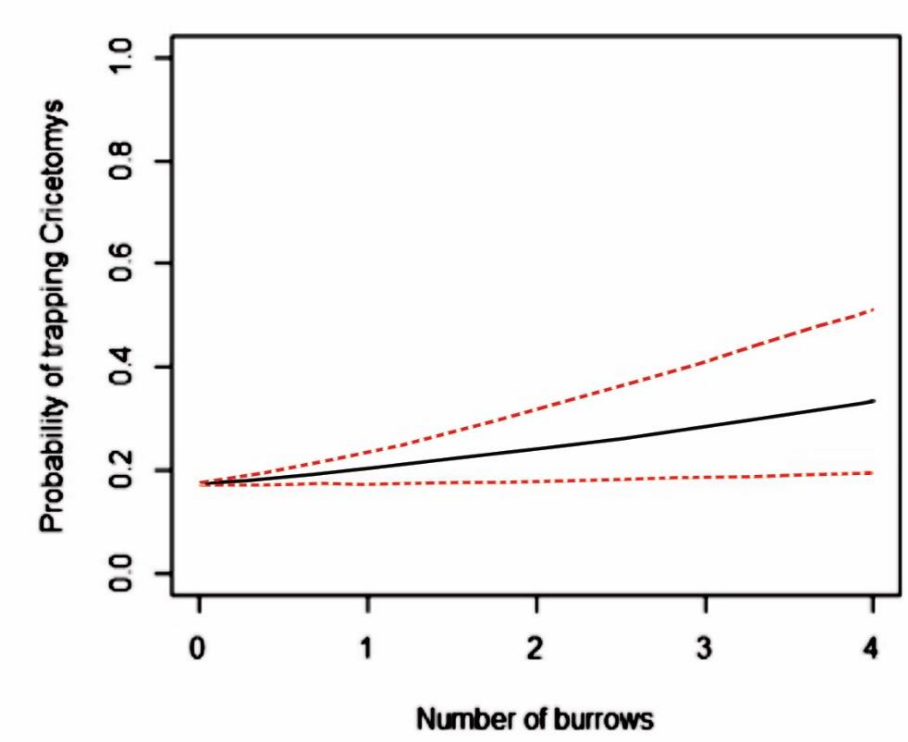

Figure 2.2: Probability of trapping *Cricetomys* per trap night in respect to the number of burrows within a 5 m radius around a trap location. The solid line is fitted through the average of capture or no capture for each value of the *Cricetomys*

burrows (with dashed lines showing 2 SE for the fitted average line — see parameter estimates in Table 2.2).

There was no significant difference in the respective head length, body length and tail length of male and female *Cricetomys* (Figure 2.3), although females were slightly heavier than males (Table 2.3). Because *Cricetomys* body masses can increase or decrease (Appendix 2.1), the slight body mass difference may not be constant. Additionally, the range of body mass for the trapped males was wider than that of the females (Figure 2.4).

Growth in *Cricetomys* body parts is generally thought to occur at the same time (Ajayi et al. 1978) however, the pairwise correlation coefficient between body parts in males was higher than that of females (Table 2.4). the body length of females was slightly negatively correlated with tail length and head length (Figure 2.5).

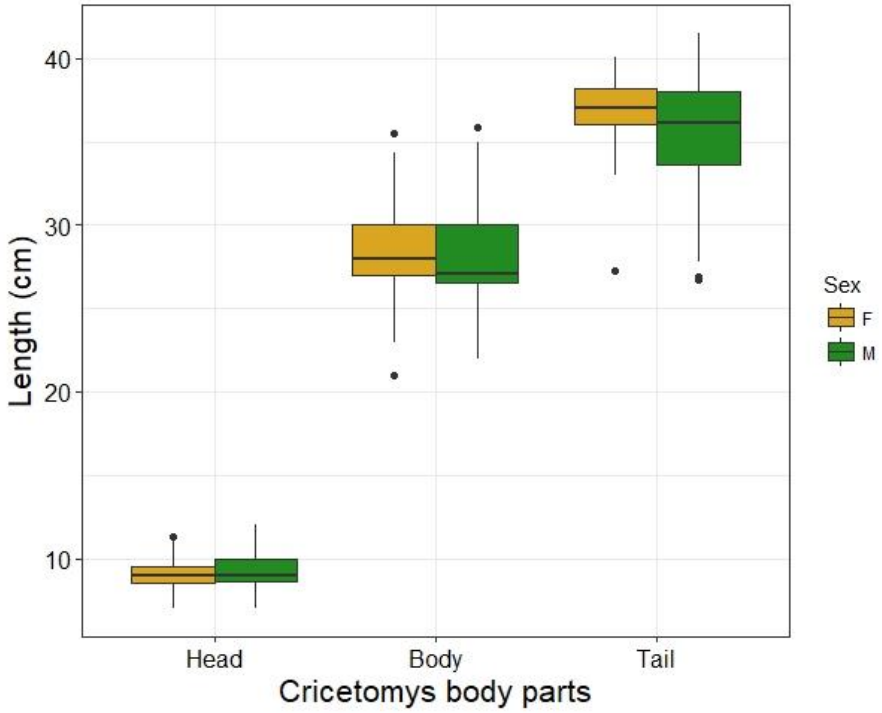

Figure 2.3: Box plot showing the length of *Cricetomys* body parts in NNFR. Green and brown boxes represent male and females respectively. Shown in the plot above are; median values (solid horizontal line), 50th percentile values (box outline) and 90th percentile values (whiskers) and outlier values (closed circles)

Table 2.3: Comparison of male and female morphological parameters (t-test). No difference between male and females except in weight. Significant p-values are denoted by an asterisk (*)

Body parameter	**Mean (male)**	**Mean (Female)**	**SE**	**df**	**t**	**P**
Head length (cm)	9.33	9.24	2.01	118.22	0.57	0.57
Body length (cm)	27.83	28.12	3.02	101.92	-0.64	0.52
Tail length (cm)	35.91	36.58	2.84	138.58	-1.68	0.1
Body mass (kg)	0.86	0.92	0.08	154.92	-2.74	0.01*

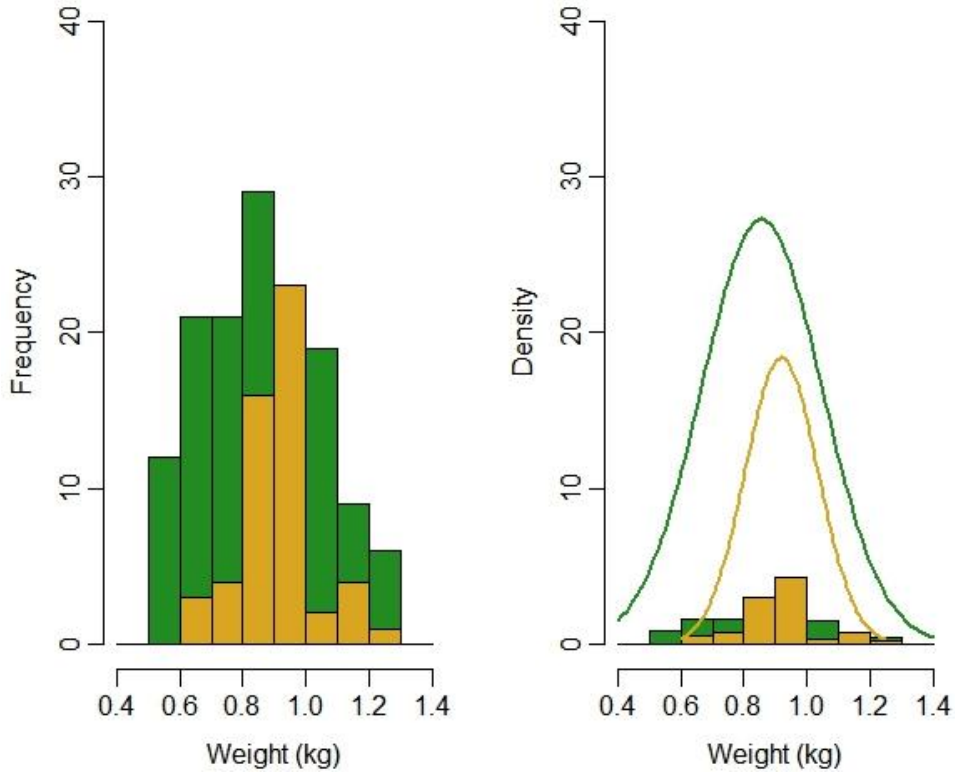

Figure 2.4: Histogram and density plots of male (green) and female (brown) *Cricetomys* body mass.

Table 2.4: Pairwise correlation of *Cricetomys* body parameters. Significant p-values are denoted with an asterisk (*)

Correlated body parts	**Sex**	**df**	**t**	**r**	**p**
Head length - Body length	M	128	3.97	0.33	0.00*
	F	51	-1.16	-0.15	0.20
Head length - Tail length	M	127	6.03	0.47	0.00*
	F	51	2.55	0.34	0.01*
Head length – Body mass	M	128	7.19	0.53	0.00*
	F	51	3.36	0.42	0.00*
Body mass - Body length	M	128	7.58	0.56	0.00*
	F	51	2.07	0.28	0.04*
Body mass - Tail length	M	127	7.37	0.55	0.00*
	F	51	0.67	0.09	0.51*
Tail length - Body length	M	127	6.12	0.47	0.00
	F	51	0.69	0.10	0.49

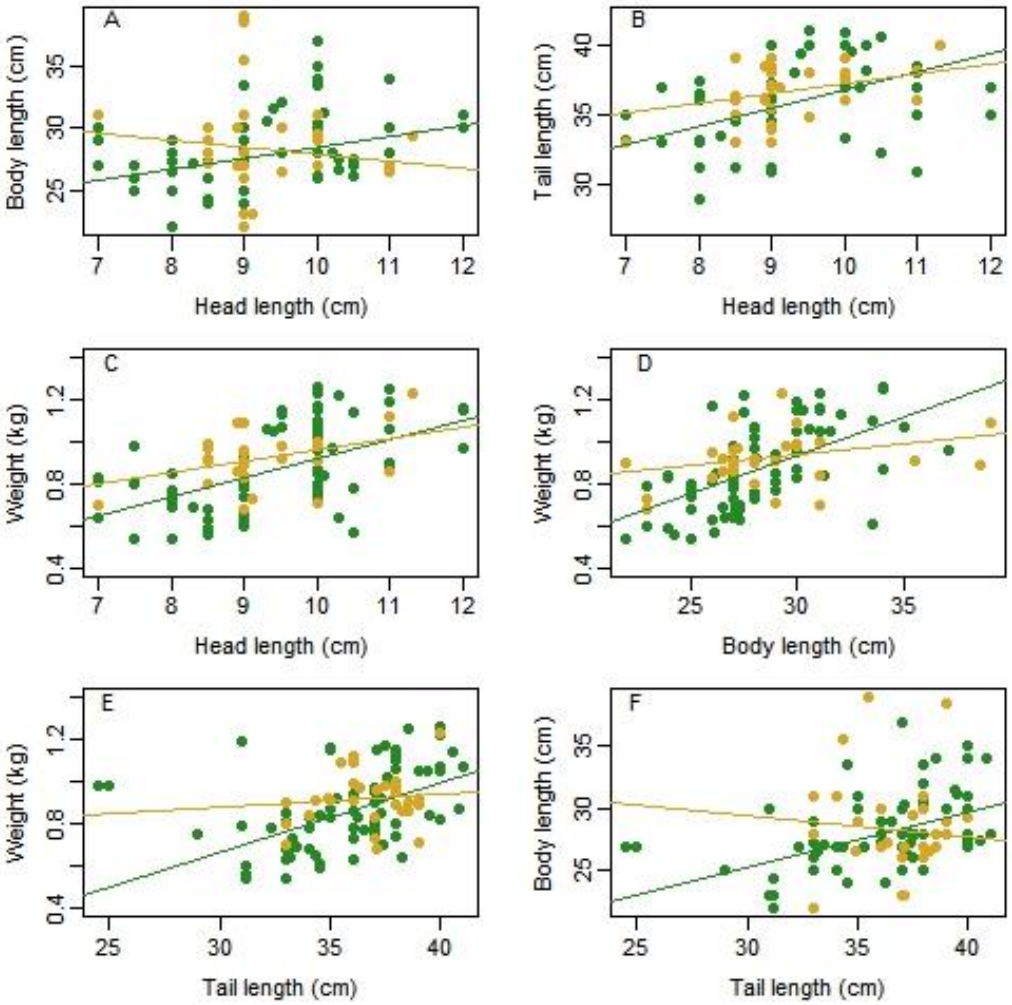

Figure 2.5: Pairwise scatterplots of *Cricetomys* morphological parameters. All correlations were positive except for female head length and body length (A) and female tail length and body length (F) (Details are shown in Table 4).

During an average of 200 camera trap nights in each habitat, 94, 14, and 5 *Cricetomys* images were recorded in the forest core, forest edge and forest fragments respectively (Figure 2.6). While no *Cricetomys* photo was captured in the grassland habitat, two photographs of barn owls (*Tyto alba*) were recorded in that habitat. The density of *Cricetomys* was highest in the forest core and lowest in the forest fragment (Table 2.5). Squirrels and porcupines were among the other rodent species in the captured images, although most of the them hardly use burrows.

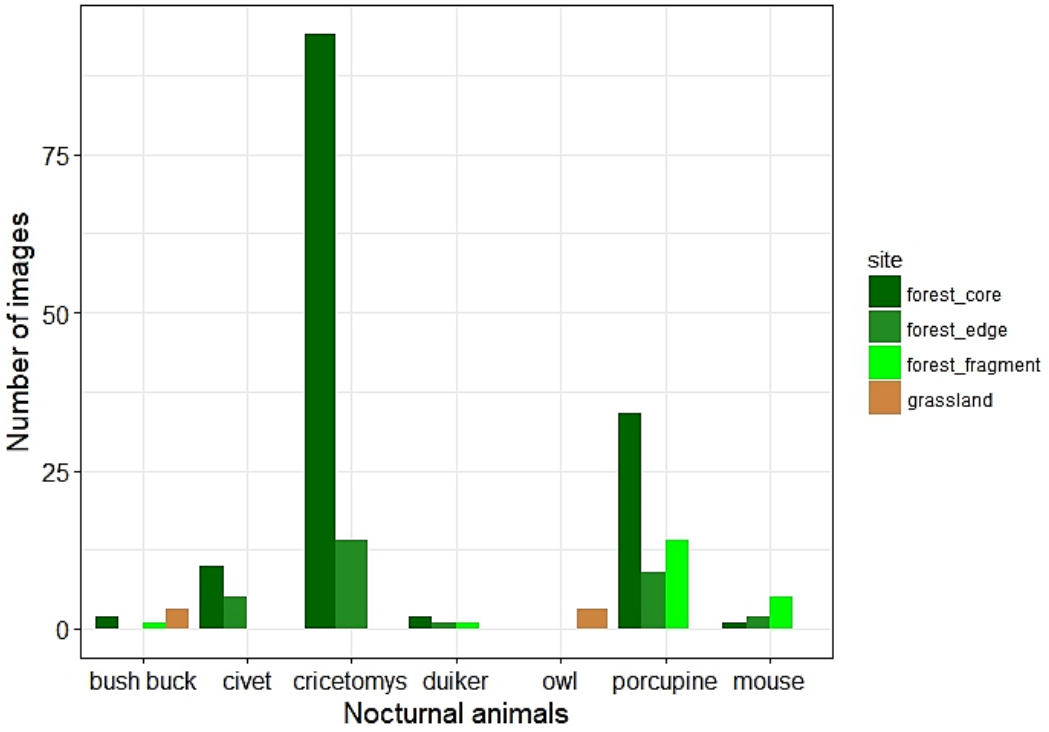

Figure 2.6: Number of nocturnal animal photographs recorded per 200 trap nights in the different habitats of NNFR.

Table 2.5: Estimated density of *Cricetomys* using REM in the different habitats of NNFR. Lcl and Ucl are the lower and upper confidence limits respectively.

Habitat	**Mean density (rats/ha)**	**Standard error**	**Lcl**	**Ucl**
Forest Core	3.308	0.557	2.195	4.211
Forest Edge	0.417	0.165	0.087	0.747
Forest fragment	0.078	0.031	0.028	0.143
Grassland	0	NA	NA	NA

The SECR results showed that of all the measured habitat variables, only the number of *Cricetomys* burrows had a likelihood of being important in predicting the density of *Cricetomys*. Number of burrows occurred most frequently in the top 20 best models (Appendix 2.2). However, the best model did not include any of the

measured habitat variables such as slope, percentage canopy cover, cover of herbs, dead logs and litter depth. Overall *Cricetomys* density, as revealed by the best SECR model was 6.29 (± 1.62) rats/ha while the overall population size estimated by the same model in the largest continuous forest patch (7.5 km^2) was ~4700 (± 1215) rats. The overall capture probability g0 as estimated from the best model was 0.31. The estimated densities at the different sessions are shown in Table 2.7. There was a significant difference between the SECR density estimates of *Cricetomys* in the two forest core sites (w=16, p=0.029); the density of *Cricetomys* in the second forest site was consistently higher than the density of rats in the first forest site (Figure 2.7). Similarly, the density of males was consistently higher than that of females (Figure 2.8).

Table 2.6: Estimated density and population size of *Cricetomys* in NNFR using SECR. N = estimated population size; standard error in parentheses. Lcl and Ucl are the lower and upper confidence limits respectively.

Period (season)	**Session**	**Density**	**Lcl**	**Ucl**	**N**	**Lcl**	**Ucl**
Dec-15 (Dry)	1	7.31 (1.78)	4.56	11.71	5482.5 (1370.6)	2741.3	8223.7
Jan-16 (Dry)	2	8.49 (1.99)	5.40	13.37	6367.5 (1532.3)	3302.9	9432.1
Apr-16 (Early wet)	3	4.24 (1.22)	2.44	7.38	3180.0 (939.4)	1301.2	5058.8
Dec-16 (Dry)	4	6.37 (1.61)	3.90	10.38	4777.5 (1239.7)	2298.1	7256.9
Jan-17 (Dry)	5	5.89 (1.52)	3.57	9.72	4417.5 (1170.4)	2076.7	6758.3

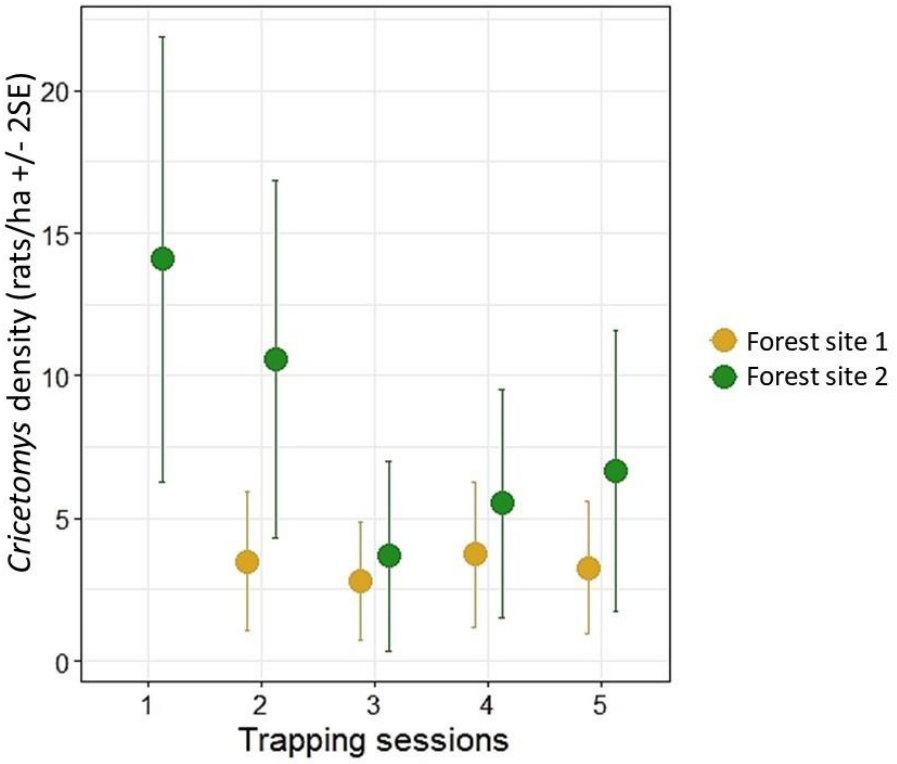

Figure 2.7: Density of *Cricetomys* in the two forest sites of NNFR. Session 3 was carried out the early wet season while sessions 1,2, 4 and 5 were in the dry season. *Cricetomys* density for the first forest site is not shown on the plot because only three individuals were trapped and at least ten capture events are needed for SECR analyses

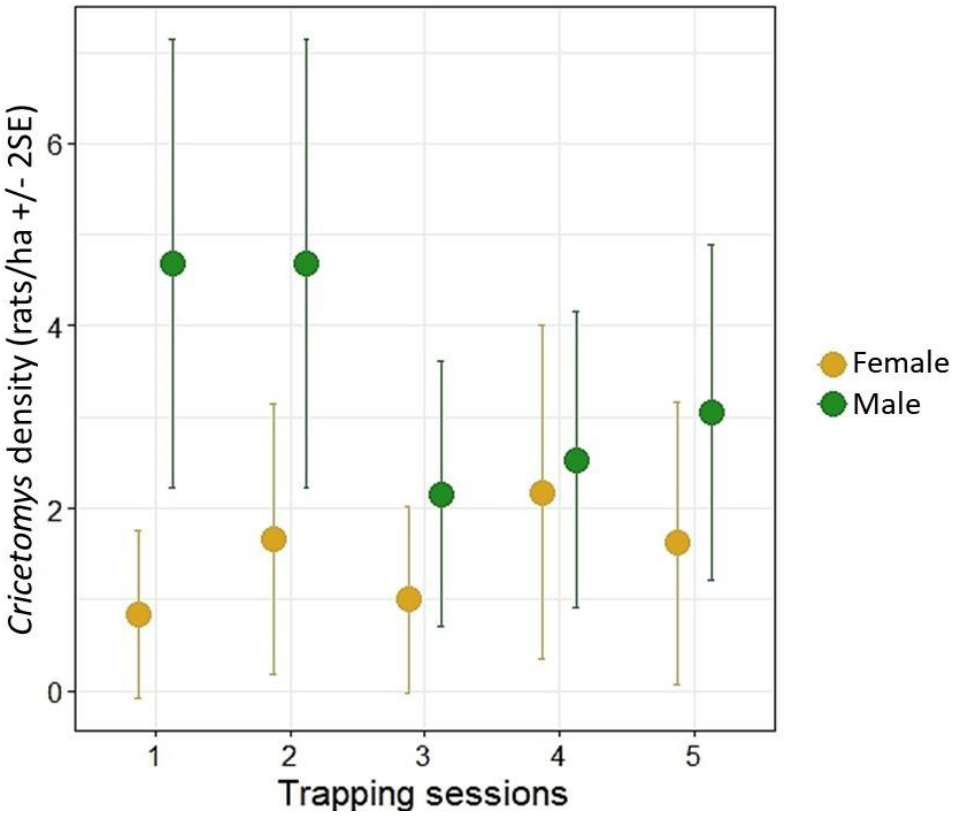

Figure 2.8: Density of male and female *Cricetomys* in NNFR. Density of males was always higher than females.

Although 55% of *Cricetomys* movement between traps as recorded in my live-trapping experiment occurred within a 50 m radius of a trap location (Figure 2.9), *Cricetomys* were observed to move up to 127m from a trap location. This indicates that their home range radius may be up to more than a 100m radius. Using a σ value of 31.45 m as determined by the SECR output, the home range area (HR_{95}) was estimated as 4.03 ha while the home range core area (HR_{50}) was 0.31 ha.

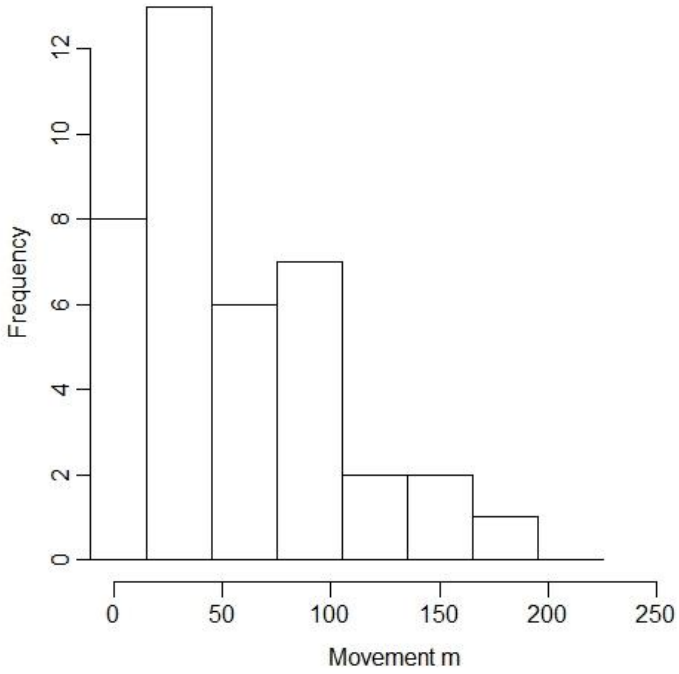

Figure 2.9: Frequency of re-captured *Cricetomys* movement distances.

The time stamp on the camera trap images revealed that *Cricetomys* were more active in the first three, and last three hours of the night (Figure 2.10). Although there was no obvious pattern of activity, two peak activity periods (19:00 - 20:00 h and 04:00 h – 05:00 h) were observed thus confirming they are nocturnal rather than crepuscular.

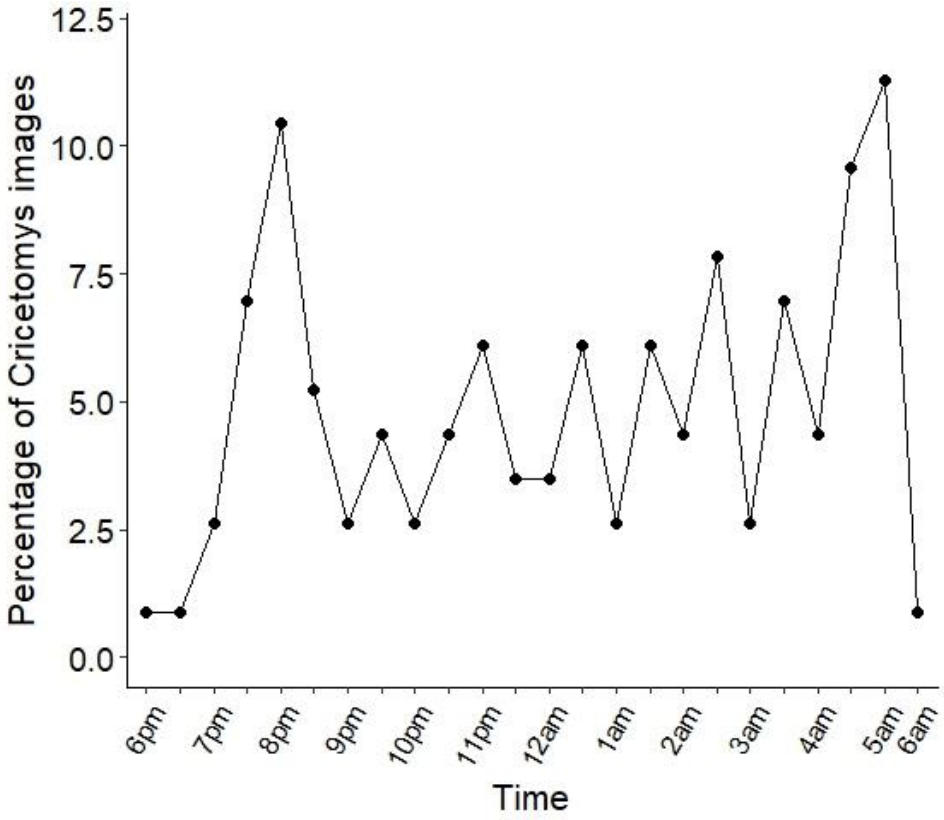

Figure 2.10: *Cricetomys* activity period in NNFR from 18:00 h – 06:00 h.

2.4 Discussion

In this study, I showed that *Cricetomys* in NNFR are most abundant in the forest core and least abundant in the grassland habitats. The mean *Cricetomys* density (6.29 rats/ha) by live-trapping and (3.31 rats/ha) by camera trapping in the forest core of this study is lower than the density of *C. gambianus* (13.4 rats/ha) reported by Fa and Purvis (1997) and may be due to a species difference. Although *Cricetomys* are more abundant in the core forest, there is an apparent spatial variation in their densities, which may be related to microhabitats that favour their presence in such sites.

2.4.1 **Microhabitats with burrows and the presence of *Cricetomys***

Among all the microhabitat variables measured within a 5 m radius of the live trap locations in my experiment, only the number of burrows was significant in predicting the presence of *Cricetomys*. One possible explanation could be that *Cricetomys* may have more burrows within the core areas of their home range. Having more burrows could potentially be useful in aiding escape from predators, and as a result, small mammals may have more opportunities of utilising the resources within their home range. Van Der Merwe and Brown (2008) for example, found that perception of predation risk by ground squirrels (*Xerus inauris*) in South Africa was lower at locations where their burrows are abundant. Although *C. gambianus* are known to have a maximum of four burrow exits in savannas and human modified landscapes (Ajayi, 1977a), the number of burrow that exits may be higher for *C.* sp. nov. in my study area because the risk of predation may be higher in the forest as many predators may also spend more time in the forested areas. Potential predators such as African golden cats (*Caracal aurata*) and African civets (*Civettictis civetta*) which have been captured by my camera traps frequently occur in the forest to avoid being hunted by humans. However, this is yet to be demonstrated.

2.4.2 ***Cricetomys* morphometrics**

The similarity in body size of male and female *Cricetomys* found in this study indicates that they are a monogamous species (Kleiman, 1977), a characteristic typical of members of the genus *Cricetomys* (Ray & Duplantier, 2013). Kleiman (1977) argued that sexual monomorphism is an evolutionary product of long term pair bonding. While observation of bonding pairs was beyond the scope of this study, (Ajayi et al., 1978) demonstrated that pair bonding is a typical characteristic of *C. gambianus*. In their experiment to determine the optimal sex ratio for *C. gambianus* in breeding cages, Ajayi et al. (1978) prepared six cages with the following sex ratio combinations (m = males; f = females); 1m:1f, 1m:2f, 1m:3f, 1m:4f, 1m:5f and 2m: 1f. In all these combinations, they found that only a single pair, bonded for the entire period of the study (three months) and only females that

bonded with a male in the cage became pregnant. It is most likely that *C.* sp. nov in my study area also exhibits pair bonding since they had similar body size. The overall body length range of *Cricetomys* sp. nov. in this study, i.e. 60-83 cm was similar to that of *C. emini,* i.e. 61-81 cm (Ray & Duplantier, 2013) and *C. gambianus* in Nigeria, i.e. 62-80 cm (Ajayi, 1977b). Although the measured body traits in male and female *Cricetomys* appeared identical, results of the pairwise comparison of the body measured traits appeared slightly different as the body parts, and body mass of males had a stronger positive correlation than females. A closer look at the pairwise comparison of male and female rats showed that the sizes of males are more variable. It is likely that younger females grow faster than the males, although their growth slows at a certain stage of maturity while that of males is continuous (see Figure 2.5). Schulte-Hostedde et al. (2001) suggested that male small mammals should have the larger muscle mass to aid intra-sexual combat and mate searching, while in contrast, females only need to grow to a certain size, after which further energetic investment is made to facilitate reproduction.

2.4.3 **Distribution of *Cricetomys* in NNFR**

While my live trapping study was impractical across the four main habitats in NNFR (i.e. forest core, forest edge, forest fragment and grassland habitats), the use of camera traps showed that *Cricetomys* abundance decreases as forest cover decreases. This suggests that *Cricetomys* sp. nov. in my study area was possibly more genetically related to *C. emini* which prefers high forests (Ray & Duplantier, 2013) than *C. gambianus*, which mostly occurs in savannas. Furthermore, using molecular and craniometric methods, Olayemi et al. (2012) showed that the new clades of *Cricetomys* species (which includes the one in this study) were more related to *C. emini* than *C. gambianus*. It is likely that *Cricetomys* sp. nov. and its close relatives which are adapted to dwelling in high forest areas may have evolved better behavioural means of predator avoidance in the forest compared with open savannahs where predators like owls have easy access on their preys. The two barn owl photographs recorded by my camera traps in the grassland suggests that the

rats seek to avoid such predators, which find their prey via echolocation, hence escape from such predators may be difficult in open areas.

Another important reason that may explain the abundance of *Cricetomys* in forest core areas is the availability of preferred food resources. Since *Cricetomys* are known predators of large seeds (Nyiramana et al., 2011; Aliyu et al., 2014; Seltzer et al., 2015), it is plausible that they will occur in places where these seeds are more abundant. Additionally, the high diversity of large-seeded species and large arthropods such as crabs in the streams of the forest core in the forest core of NNFR (pers. obs) should potentially provide food for the rats at different periods of the year.

The camera traps recorded no *Cricetomys* in the grassland, and out of the six individuals captured in the grassland-forest edge habitat during the live-trapping experiment (see Table 1), only one was captured in the grassland, and this was less than 20 m away from the forest edge. This suggests that the rats may infrequently extend their range to the adjacent grasslands for foraging or other activities.

2.4.4 **Uneven density of *Cricetomys* in the forest core**

The repeated live-trapping experiments at two different sites in the forest revealed that *Cricetomys* density was higher in some core sites than others. Apart from obvious differences in vegetation structure (e.g. forests and grasslands), spatial differences in tree species assemblage may also have an effect on small mammal community composition and abundance (Williams et al., 2002). Although I did not consider the tree community within the live-trapping grids of my experiment for logistic reasons, it is possible this was a factor affecting the abundance of *Cricetomys* at different sites within the forest core. Niche partitioning as a result of competition may also have an effect on the density distribution of *Cricetomys*, but my study was not designed to test that. Considering the short range at which *Cricetomys* individuals were re-trapped, it is very likely that these rats are territorial. The ideal despotic distribution (IDD) theory (Fretwell, 1972) proposes that dominant individuals will secure high-quality habitats and is expected among small territorial

mammals. This could be an underlying mechanism of *Cricetomys* density distribution, and thus, smaller high-quality areas could be monopolised by dominant individuals ultimately resulting in higher population densities within high-quality patches. Similar to IDD, another possible explanation for higher densities of *Cricetomys* in some forest patches may be a positive density dependence (the allee effect) effect (Morris 2002). Morris (2002) demonstrated that the allee effect explained the distribution of the red-backed voles (*Clethrionomys gapperi*) in Canada, but there is little or no evidence to suggest that it is the underlying mechanism regulating the spatial distribution of small mammals in the tropics; this hypothesis needs to be tested in the tropics.

Athough the live-trapping sessions occurred over a year, none of the marked *Cricetomys* individuals were trapped at both sites of the forest core; an indication that site fidelity is also a possible characteristic of *Cricetomys*. Site fidelity has been reported among other tropical rodents, including the dusky rats (*Rattus colletti*) of Australia (Madsen & Shine, 1999) and the orange-rumped agouti (*Dasyprocta leporina*) of French Guiana (Dubost, 1988). However, some tropical rodents, e.g. the red acouchy (*Myoprocta exilis*) of French Guiana (Dubost, 1988) and the central American spiny rats (*Proechimys semispinosus*) of Panama (Seamon & Adler, 1999) are not territorial and do not exhibit any evidence of site fidelity.

I found that there is a possible annual population density cycle of *Cricetomys* in NNFR because the density of rats recorded in the dry season (December and January) in both 2015/2016 and 2016/2017 were higher than the density of rats recorded in the early part of the wet season (April 2016) in the two forest core sites. Annual changes in tropical small mammal populations have been associated with changes in rainfall pattern (Madsen & Shine, 1999; Lima et al., 2001; Lima et al., 2003, Bryom et al., 2014). While it is possible to link seasonal climatic changes with *Cricetomys* population dynamics, it was not clear whether there is seasonal variation in predator abundance that may affect the population cycles of *Cricetomys*. It is also possible that behavioural changes, which come with food

abundance may obscure my interpretation of population cycles in *Cricetomys*. For example, from the yearly tree phenology data recorded in NNFR, most tree species fruit at the beginning of the rainy season (NMFP Weather data) and so, abundant food supply may limit the spatial range of activities as rats spend more time at their food sources. Thus, rats may hardly encounter the traps which are widely spread out.

2.4.5 **Uneven densities of male and female *Cricetomys***

Apart from spatial variability, I also found that the density of trapped males was higher than that of females. I propose two possible explanations for this finding: i) males are disproportionately higher in the population, or ii) behavioural differences between males and females result in differences in detection. The primary source of a sex-structured population among mammals is the manipulation of offspring sexes at birth. While this has been demonstrated for some small mammals in the laboratory (see review in Clutton-Brock & Iason, 1986), there is apparently no report of biased sex ratios in small mammal offspring in tropical forests. Some authors (e.g. Buskirk & Lindstedt, 1989; Smith, 1989) argue that part of the reason for rare captures and increased longevity of female small mammals is that males of most species are higher risk-takers. A possible difference in behaviour between male and female *Cricetomys* in terms of risk taking while foraging may have affected my results. Additionally, because some pairs of monogamous small mammals, e.g. elephant shrews *Rhynchocyon chrysopygus* and *Elephantulus rufescens* have completely overlapping home ranges yet forage solitarily (Rathbun, 1979), it is possible that *Cricetomys,* which has shown some monogamous traits, may also have overlapping home ranges. Therefore, if males are more active within the home range than females, then it is likely that they will be trapped at a higher frequency than females within the same area. Alternatively, a combined scenario whereby *Cricetomys* has a male-dominated offspring ratio at birth which will eventually be balanced by predation is also possible, but there is no evidence for that yet.

2.4.6 **Spatial movement of *Cricetomys***

Although there is apparently no report of the home range size for *Cricetomys emini* which is closely related to *C.* sp. nov in my study area, the home range size of *C. gambianus* in the southern African subregion is known to be between 2.2 ha and 11 ha with a mean of about 5 ha (Ray & Duplantier, 2013). My study is one of the few, if not the first, to estimate the home range size of *Cricetomys* in tropical montane forests; showing the home range of *Cricetomys* in NNFR overall to be about 4 ha wide, but the home range core (where it most frequently occurs) was about 0.3 ha. This agrees with Engeman et al. (2006) that the home ranges of *Cricetomys* are smaller in their native habitats. The fact that about half of the recaptured individuals were captured within a 50 m radius of the trap locations also suggests that *Cricetomys* in NNFR generally have a small range. However, the changes in the maximum distances between trap locations during the different trapping sessions also suggest that *Cricetomys* in NNFR can easily extend their home ranges when necessary.

2.4.7 ***Cricetomys* activity pattern**

In this study, I found that *Cricetomys* is more active in the early part of the night (7 pm – 8 pm) and the early hours before dawn (4 am – 5 am). This is contrary to my prediction that the rats will be more active in the first half of the night as has been observed by (Oliveira-Santos et al., 2008). Since many small mammals are more active at night as an anti-predation strategy (Gómez et al., 2005), I expected *Cricetomys* to be more active at midnight when it is darkest because they are almost totally inactive when the moon is bright (pers. obs), suggesting that they prefer darker nights. The activity period of *Cricetomys* in this study may be important as a strategy for predator avoidance or to reduce competition. Synchronous activity period as a predator avoidance strategy has been demonstrated by Lambert et al. (2009). In their study, they showed that the activity periods of agoutis (*Dasyprocta punctata*) contrast with that of nocturnal ocelots (*Leopardus pardalis*) which are known to be the main predators of agoutis. Because African brush-tailed porcupines (*Atherurus africanus*) occur in NNFR and may be

potentially competing with *Cricetomys* for food resources, it is possible that *Cricetomys* activity period observed in this study may be useful in reducing competition.

2.5 Conclusion

Overall, this study has shown that *Cricetomys* in NNFR mostly occured in the forest core and that their density in the forest core was not even. This study shows that the population density of the rats may be annually cyclical. Despite having monogamous traits, *Cricetomys* males seem to occur at a higher density compared to females. Finally, I have shown that *Cricetomys* in NNFR may have peak periods of activity in the night and this may be useful for them to avoid predators or reduce competition.

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Effect of food availability on the abundance of African giant pouched rat (*Cricetomys sp*. nov.) in Ngel Nyaki Forest Reserve, Nigeria.

Abstract

It is generally agreed that food availability plays a key role in the spatial distribution of rodents. However, little is known about its effect on the density of the ecologically important African giant pouched rat (*Cricetomys spp*) in Afromontane forests. In this study, I predicted a positive correlation between the density of African giant pouched rats and large-seeded tree species (as a proxy for food availability) in a tropical West African montane forest—Ngel Nyaki Forest Reserve, Nigeria. I estimated the density of rats using two methods: i.) camera traps with a random encounter model (direct method) and ii.) intensive burrow searches (indirect method). Although results from the first rat survey method did not support my prediction, the density of rat burrows was correlated positively with the density of large-seeded species. This result suggests that a high density of large-seeded trees is likely to support a high density of African giant pouched rats in the long term, but may not be important in the short term, especially during periods of food scarcity.

3. 1 Introduction

For animals, food resources are often spatially and temporally distributed in patches of varying qualities (Hamilton, 2010). Because animals tend to occur where their food sources are abundant, their patterns of occurrence may often resemble their food distribution pattern (Stephens & Krebs, 1986). Although many factors such as weather, disease, water, predation and food supply may determine the distribution of animals, food and predation frequently appear to be the key factors (Korpimäki et al*.,* 2004; Krebs, 2009; Prevedello et al., 2013).

Given the temporal and spatial distribution of food in most ecosystems, there are costs (e.g. predation risk and energetic requirements) associated with finding food (Bernstein, 1975; Hamilton, 2010). The optimal foraging theory proposes that an animal can effectively maximise its fitness by foraging when the cost is low, and the benefits or energetic rewards are high (Sinervo, 1997). Charnov (1976) proposed the marginal value theorem for optimal foraging, which states that the travel time to a food patch influences foraging time within the patch (see Figure 3.1), suggesting that animals may spend more time foraging at a low-quality food patch even when high-quality patches are available. To reduce the chances of spending time in low quality habitats, animals prefer habitats with abundant food resources, thus following the prediction of the marginal value theorem for optimal foraging (Gittleman & Harvey, 1982; López-Bao et al., 2010; Powers & McKee, 1994; Schradin & Pillay, 2006; Zubiri & Gottelli, 1995). This strategy enhances their chances of finding high-quality food and reduces their travel time to food patches thereby minimising predation risk and allowing time for other activities, such as breeding.

Selection of habitats with abundant food resources is especially important for animals that invest a lot of time and energy in nest building. For example, the northern anteater chat (*Myrmecocichla aethiops*), which makes its nest by burrowing tunnels on sides of eroded gullies or abandoned wells, has been shown to select habitats which support its preferred prey items (ants and termites) in abundance (Yadok et al., 2014). Similarly, Kent & Dorea (1984) showed that Brazilian insectivorous mammals, select habitats that support abundant termites. Because food abundance is often temporally variable, many animals migrate from their home ranges in periods of scarcity (Alerstam et al., 2003). However, migration is impractical for most small mammals due to the high energy demand and the predation risk involved (Hanski et al., 2001). Thus, small mammals often respond to periods of scarcity by increasing the size of their home ranges (Schradin & Pillay, 2006).

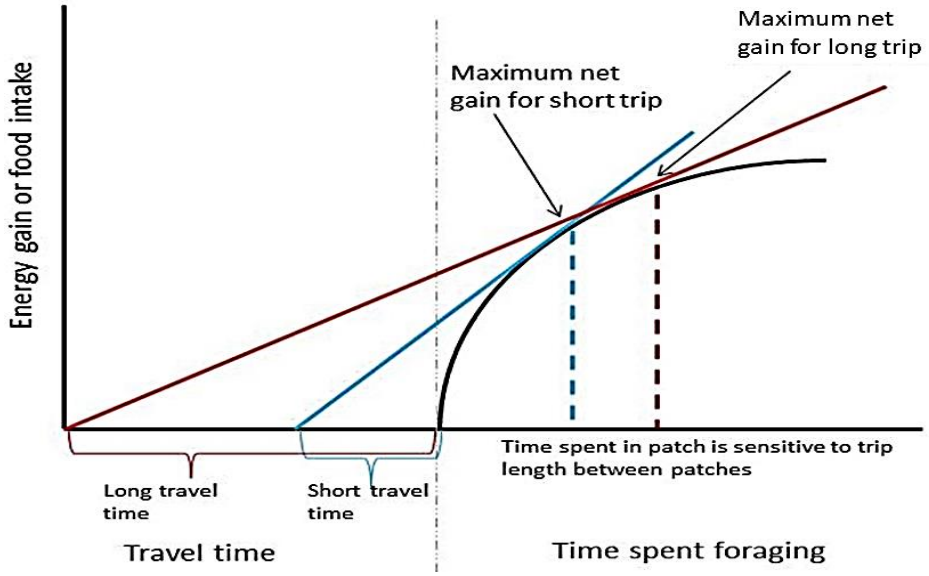

Figure 0.1: An illustration of the marginal value theorem (adapted from Sinervo 1997). A Longer travel time to food patches often results in a longer foraging time. Home ranges with abundant food supplies can effectively reduce travel time and increase utilization of other food patches.

3.1.1 Food availability and the density of small mammals

Population densities of small mammals in most habitats fluctuate annually, or multi-annually (Banks & Dickman, 2000; Batzli, 1992; Krebs & Myers, 1974) and the key extrinsic factors that influence these cycles are food and predation (Krebs, 1996; Krebs et al., 1995). In many studies, food abundance cycles have been shown to drive fluctuations of small mammal populations (Adler, 1998; Banks & Dickman, 2000; Bergallo & Magnusson, 1999; Taitt, 1981; Turchin & Batzli, 2001). Food availability may have a bottom-up effect on small mammal populations as commonly observed in consumer-resource systems where an abundance of prey results in the abundance of predators and vice versa (Volterra, 1926; Lotka, 1956). By modelling and testing the effect of food availability on the population dynamics of rodents in Alaska, Turchin & Batzli (2001) showed that food abundance is important in determining the density of these rats. Apart from improving body

condition and reproduction in small mammals (Banks & Dickman, 2000; Bergallo & Magnusson, 1999), food abundance has also been shown to increase their survival rates (Krebs et al., 1995). For small mammals that depend on fruits and seeds for their survival, maintaining home ranges around the preferred tree species is critical for taking advantage of periodic food abundance (Bergallo & Magnusson, 1999). In an experiment to determine how changes in spatial abundance of fruiting trees affect the habitat and space use of red squirrels (*Sciurus vulgaris*) in Northern England, Lurz et al. (2000) found that spatial clusters of fruiting trees were important for territory locations in red squirrels. Lurz et al. (2000) also showed that high-quality sites (i.e. habitats with abundant fruiting trees) supported a higher density of red squirrels compared with sites where these trees were sparse. Distribution and occurrence of small mammals in relation to trees that provide them with food have also been demonstrated in tropical scatterhoarding rodents (Aliaga-Rossel et al., 2008; Jorge & Peres, 2005).

3.1.2 Distribution of tropical scatterhoarding rodents and their associated food items

Although there are many factors affecting the distribution of tropical scatterhoarding rodents (August 1983; Mares & Ernest, 1995), the density of trees that provide them with food has been shown to have a major influence on the distribution of these rodents (Cid et al., 2013; Emsens et al., 2013; Jorge & Peres, 2005; Silvius & Fragoso, 2003). Given the seasonal fruiting phenology of most tropical trees species (Chapman et al., 2005; Frankie et al., 1974; Singh & Kushwaha, 2005; Snow, 1965), it is expected that home ranges and densities of tropical scatterhoarding rodents should be seasonal and rodent densities should be higher at forest sites with diverse large-seeded fruiting tree species (Jorge & Howe 2009). This is because a more tree-diverse site may provide a cumulatively longer period of food supply for scatterhoarding rodents because fruits of the different species may ripen at different periods of the year. On the contrary, scatterhoarding rodents have been shown to maintain their home ranges across seasons (Aliaga-Rossel et

al., 2008), but home range sizes increase in periods of scarcity and decrease in periods of food abundance (Jorge & Peres, 2005).

Higher densities of scatterhoarding rodents occur in habitats with an abundance of large seeded species (Jorge & Peres, 2005; Silvius & Fragoso, 2003). For example, Jorge and Peres (2005) showed that the red-rumped agouti (*Dasyprocta leporina*) occurred at higher densities in forest sites that had many Brazil nut (*Bertholettia excelsa*) trees. Similarly, Aliaga-Rossel et al. (2008) showed that the Central American agouti (*D. punctata*) preferentially occurs at higher densities in forest sites with many *Astrocaryum* trees. Scatterhoading rodents generally prefer large seeds because they offer higher energy rewards and they can easily be located (Forget et al., 1998). Distribution patterns of scatterhoarding rodents in the Neotropics may differ from the Afrotropics, but very little is known about the distribution of scatterhoarding rodents in the Afrotropics.

3.1.3 Distribution of Afrotropical scatterhoarding rodents

In comparison with the Neotropics, studies of scatterhoarding rodents in tropical Africa are very recent (Nyiramana et al., 2011; Aliyu et al., 2014; Seltzer et al., 2015; Rosin & Poulsen, 2017). Of these few studies, none have investigated the effect of large-seeded tree species on the distribution of scatterhoarding rodents. Knowing the distribution of scatterhoarding rodents in relation to tree species occurrence is critical for understanding how quickly these rodents find seeds and the distance to which they disperse seeds (Aliaga-Rossel et al., 2008). Additionally, it can provide information on how these animals cope with the seasonal fluctuations in food resources (Ylönen, Pech, & Davis, 2003).

The African giant pouched rat (*Cricetomys* sp. nov) has recently been demonstrated to scatterhoard large seeds of different tree species (Aliyu et al., 2014; Nyiramana et al., 2011; Seltzer et al., 2015). Considering its relatively large size (~ 1 kg) and scatterhoarding behaviour, the African giant pouched rat may play an important role in seed dispersal of large-seeded tree species. This is likely to have become more important following the loss of large-bodied mammals (e.g. elephants and

chimpanzees) which dispersed large-seeded tree species in the past (Aliyu *et al*., 2014; Nyiramana *et al*., 2011; Seltzer *et al*., 2015). However, little is known about the occurrence of these rats in relation to the distribution of large-seeded forest species.

My aim in this study was to determine the effect of the abundance of large-seed tree species (used as a proxy for food availability) on the density of African giant pouched rats in a West African montane forest —Ngel Nyaki Forest Reserve (hereafter referred to as NNFR), Nigeria. I predicted that African giant pouched rats (hereafter referred to as *Cricetomys*) would occur at higher densities in forest patches with abundant large-seeded tree species.

3.1.4 Predictions

The investigation is driven by the following predictions:

i. A higher density of *Cricetomys* would be observed at forest sites with abundant large-seeded tree species than sites with less abundant large-seeded tree species because the former sites potentially provide more food (seeds) for the rats.

ii. A higher density of *Cricetomys* would be observed at forest sites with more diverse tree species than forest sites with less diverse tree species because of the differences in fruiting periods among tree species.

iii. A higher density of *Cricetomys* would be observed at forest sites with large-sized trees that are expected to produce higher fruit yields and have larger canopies that allow more activity at such sites.

iv. Biotic factors (e.g. tree size and tree diversity) would have a stronger effect on *Cricetomys* density than abiotic factors (e.g. slope, rock cover and water source).

3.2 Methods

To investigate the relationship between *Cricetomys* and the distribution of trees in NNFR, I set up sampling locations in four large plots (60 m x 60 m) and 50 small plots (20 m x 20 m). The large plots provided the opportunity to combine both direct (camera trap surveys) and indirect (intensive burrow searches) methods of determining *Cricetomys* density while the smaller plots provided an increased sample size for the study. The large plots were in the south of the largest continuous part of the reserve, and the small plots were randomly selected across the entire continuous forest as shown in Figure 3. 2.

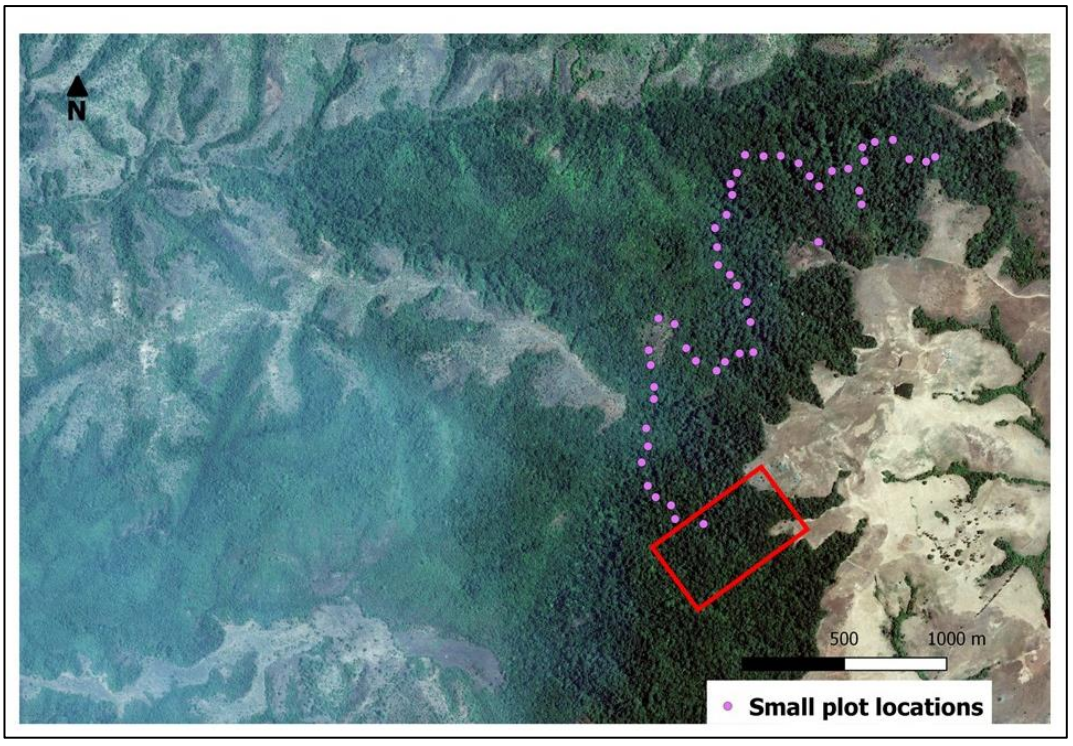

Figure 0.2: Google satellite image (2017) showing the location of the large plots (red box) and locations of the small plots (purple dots) in the largest continuous forest within NNFR (Dark green patch). Brighter regions on the right are overgrazed grasslands. Black triangle with 'N' at the top left corner indicates the North direction.

3.2.1 Large plots

To identify areas in the forest with an abundance of five common large-seeded species in NNFR, the large experimental plots, which were all located within the 20.28 ha plot of the recently established Centre for Tropical Forest Science-Forest Global Earth Observatory (CTFS-ForestGEO; www.forestgeo.si.edu) were used. The CTFS plot in NNFR is among a network of 63 plots designed to produce worldwide comparable data on tree species distribution. Within the CTFS-ForestGEO plot, every tree with a diameter at breast height (DBH) > 1 cm was mapped. Using the map of the plot (Appendices 3.1 — 3.3), it was easy to identify the locations of the large-seeded tree species when the maps of the different large-seeded species were overlaid on one another. The distribution of five most abundant large-seeded species which are known to be eaten by *Cricetomys*, i.e. *Anthonotha noldae*, *Carapa oreophila*, *Garcinia smeathmanii*, *Santiria trimera* and *Pouteria altissima* was used as the criteria for selecting plots with a high and low abundance of large-seeded trees. Because fruit availability is dependent on tree size (Chapman et al., 1992), I selected trees that were >10 cm DBH (see Gentry, 1988). I marked out four 60 m x 60 m plots, two with high abundance of large-seed trees and the other two with low abundance of large-seeded trees. Characteristics, which include the Shannon-Weiner diversity index for all tree species > 10 cm DBH of the four selected plots are shown in Table 3. 1. Each plot was at least 80 m from the plot nearest to it.

Table 0.1: Characteristics of the four large selected plots in Ngel Nyaki Smithsonian plot. Tree diversity refers to Shannon-Weiner diversity index (H).

Sites	Tree diversity (H)	Number of trees	Number of large-seeded trees	Mean diameter at breast height (cm)
High abundance plot 1	2.51	912	445	36.19
High abundance plot 2	2.64	1017	407	32.95
Low abundance plot 1	2.75	822	287	30.57
Low abundance plot 2	2.71	844	291	32.97

*****High and low abundance refers plots refers to high and low abundances of large-seeded tree species respectively

3.2.2 Camera trapping and burrow survey

To estimate the density of *Cricetomys* in the large plots, I combined the use of camera traps and intensive searches for rat burrows within the plots. I randomly placed five motion-triggered camera traps (Bushell® Trophy cam and Moutlrie® cam) in each plot such that each camera was at least 15 m away from the nearest neighbour camera. Cameras were operated for ten consecutive nights in September 2016; this ten-night camera trapping session was repeated in October and November of the same year; the transition period between the rainy and dry seasons. After each camera trapping session, images were retrieved from the camera and the cameras were placed randomly at different locations within each plot to increase the chances of capturing rat images in different territories. I used a random encounter model—REM (Rowcliffe *et al*., 2008; see details in Chapter 1) to estimate the density of *Cricetomys*.

To sample rat burrows within each large plot, I randomly laid five 5 m x 5 m plots which were at least 20 m apart. Within each of the five plots, I laid out three smaller

2 m x 2 m plots and intensively searched for *Cricetomys* burrows within the smaller plots. Only burrows that were between 4.5 cm and 15 cm in diameter were counted, to reduce the chances including other animals' burrows (Ajayi, 1977). The man number of rat burrows per meter square was used as the estimated density of rat burrows for each large plot.

3.2.3 Small plots

To determine the factors that may affect the number of *Cricetomys* burrows across the entire patch of continuous forest 50 small plots (20 m x 20 m) were laid out on a random path that ran from north to south through the forest core (see Figure 2). To ensure independence of samples, the distance between any two plots was at least 50 m. In each of these plots, the ten largest trees were identified (see Appendix 3.4), and their diameters at breast height (DBH) were measured. I used the seed size data of the Nigerian Montane Forest Project to classify species as either large- (≥ 12 mm) or small- (≤ 11 mm) seeded. In each plot, I recorded the slope and distance to the nearest stream. Also, I estimated percentages of rock cover, canopy cover and understory herbs. Using a GPS device (Garmin® GPSMAP), I recorded plot locations and elevations. Finally, using the same method of intensive burrow search in the large plots above (section 2.3.1.1), I estimated the density of *Cricetomys* burrows.

3.2.4 Statistical analyses

I compared the densities of *Cricetomys* in plots with high abundance of large-seeded trees to plots with low abundance of large-seeded trees using a Mann-Whitney U-test. The densities of *Cricetomys* burrows in both high abundance and low abundance plots of large-seeded trees were also compared using a Mann-Whitney U test. Considering the difference in the characteristics of each large plot, I tested whether there was a relationship between *Cricetomys* density and i) the abundance of large-seeded trees, ii) tree diversity and iii) and tree size using Spearman's correlation test. The same test was applied to determine whether there was a relationship between the density of *Cricetomys* burrows and these three

characteristics. To test the relationship between the density of *Cricetomys* burrows and other measured habitat variables in the small plots, I used a Pearson correlation test. Finally, a general linear model (GLM) was used to determine factors that affect the density of *Cricetomys* burrows in the small plots.

3.3 Results

3.3.1 Density of *Cricetomys* in large plots

An overall density of 4.67 (± 2.53) rats/ ha was estimated from a total of 387 *Cricetomys* images captured in 600 camera trap nights within the large plots. The overall mean density of rat burrows in the large plots was 0.02 (± 0.01) m^{-2}. Images of other animals captured by the camera traps include millipedes, birds, porcupines (*Atherurus africanus*), squirrels, pangolins, Nile monitor (*Varanus niloticus*), snakes, squirrels, duikers and chimpanzees.

The density of *Cricetomys* in the plots with abundant large-seeded species was not significantly different from the plots which had fewer large-seeded species (U = 4, p = 0.33). Similarly, there was no statistically significant difference in the density of rat burrows between plots with abundant large-seeded species and plots with fewer large-seeded species (U = 3.5, p = 0.41). Additionally, there was no correlation between the density of rats, and the density of rat burrows in the large plots (r = -0.31, p = 0.68) (Figure 3.2.). The densities of *Cricetomys* and their burrows in the large plots are summarised in Table 3.2. There was no correlation between *Cricetomys* density and; tree abundance (r= 0.82, p = 0.34), tree diversity (r= 0.76, p = 0.38), nor tree size (dbh) (r = 0.80, p = 0.33) in the large plots (Figure 3.3).

Table 0.2: Density of *Cricetomys* and their burrows in the large plots (Standard errors are shown in parenthesis).

Sites	***Cricetomys* density (individuals ha^{-1})**	**Density of *Cricetomys* burrows (burrows m^{-2})**
High abundance site 1	4.18 (±1.339)	0.04 (±0.013)
High abundance site 2	3.41 (±1.729)	0.020 (±0.015)
Low abundance site 1	6.82 ± (3.775)	0.020 ± (0.005)
Low abundance site 2	4.30 ± (2.262)	0.015 ± (0.010)

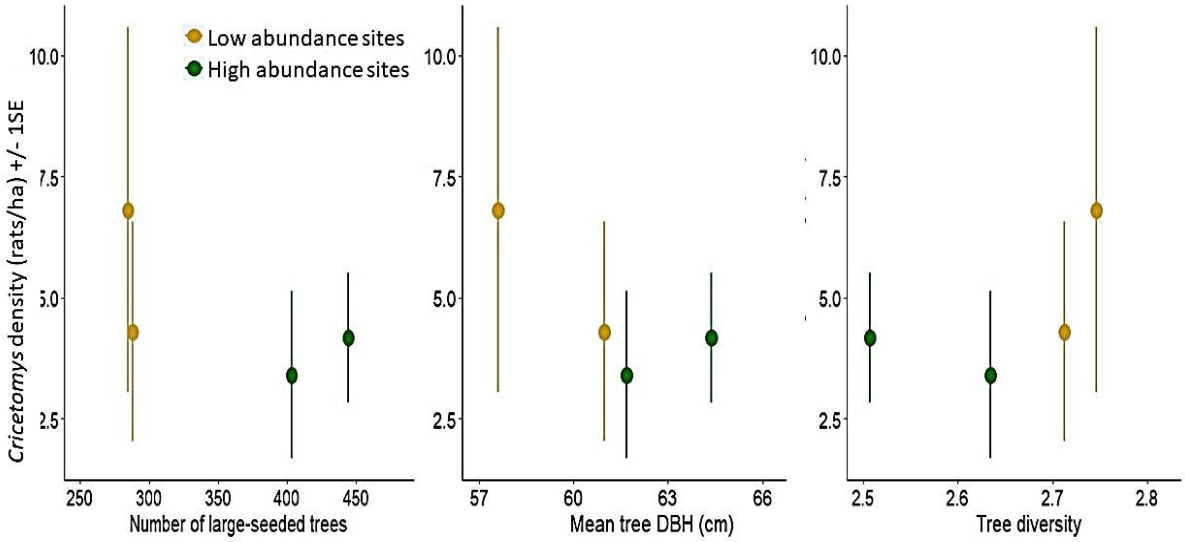

Figure 0.3: Density of *Cricetomys* (estimated using cameras) in relation to large-seeded tree abundance, mean tree size (all species) and diversity of trees (all species) in the large plots. *Cricetomys* density has no significant relationship with the distribution of trees in the large plots. (points show the mean values while the extended vertical lines show the standard errors).

A similar trend of no correlation was observed between the density of rat burrows and; tree abundance (r=-0.61, p = 0.37), tree diversity (r=-0.63, p = 0.40), and tree size (dbh) (r=-0.58, p = 0.4) in the large plots (Figure 3.4).

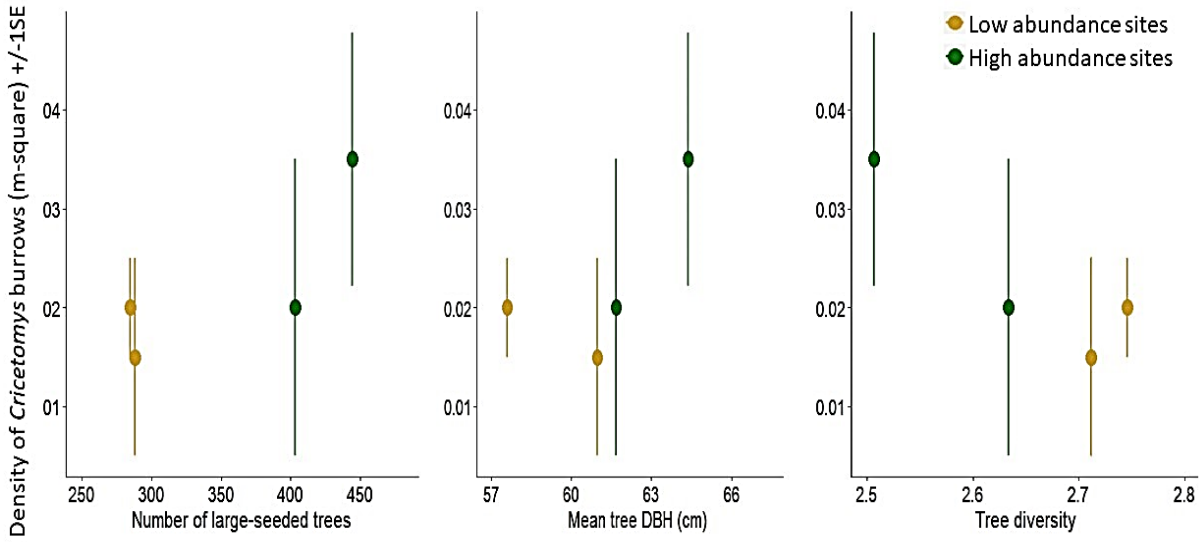

Figure 0.4: Density of *Cricetomys* burrows in relation to large-seeded tree abundance, mean tree size (all species) and diversity of trees (all species) in the large plots. The density of *Cricetomys* burrows have no significant relationship with the distribution of trees in the large plots (points show the mean values while the extended vertical lines show the standard errors).

3.3.2 Density of *Cricetomys* burrows in small plots.

The overall density of rat burrows in the small plots was 1.05 ± (0.10) m^{-2}. In this case, a significant positive relationship was found between the density of rat burrows and the number of large-seeded species (r = 0.35, p = 0.01) (Figure 3.5), There was, however, no significant relationship between the density of rat burrows and average size of all tree species combined (r = -0.07, p = 0.61), or the density of rat burrows and tree diversity of all species (r = 0.22, p = 0.13) (Appendix 3.5). Although there was a significant negative relationship between the density of rat burrows and small-seeded species (r = 0.35, p = 0.01); this was simply the converse of the result for the large-seeded trees, given that only 10 of the largest trees were

recorded in each plot. No other recorded habitat variables had a statistically significant relationship with the density of rat burrows ($p > 0.05$) (Table 3.3).

Table 0.3: Results of Pearson correlation analyses between the density of rat burrows and recorded habitat variables at small plots (400 m^2). Significant values are shown by an asterisk.

Variable	**Correlation coefficient**	**Df**	**t value**	**p value**
Number of large-seeded trees	0.35	48	0.56	0.01*
Average tree size (DBH)	-0.07	48	-0.51	0.61
Tree diversity (H)	0.22	48	-1.53	0.13
Elevation (m)	0.16	48	-1.18	0.24
Number of small-seeded trees	-0.35	48	-2.61	0.01*
Percentage bare rock	-0.02	48	-0.17	0.87
Distance to nearest stream (m)	-0.03	48	-0.24	0.81
Slope	0.13	48	0.91	0.36
Canopy Cover	0.04	48	0.29	0.77
Percentage herb cover	0.09	48	0.64	0.52

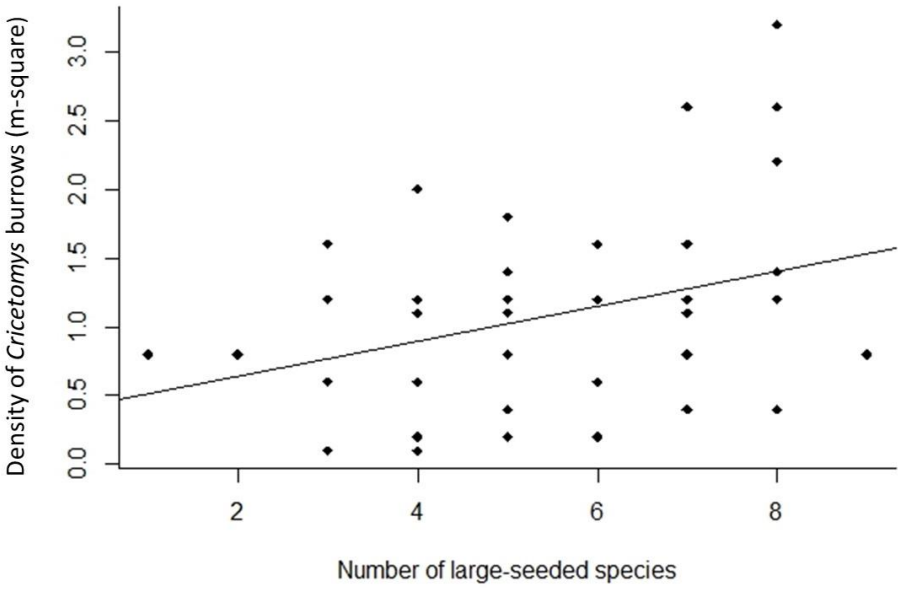

Figure 0.5: The relationship between density of *Cricetomys* burrows and the number of large-seeded species in small plots (400 m^2). Each point represents burrow density in a small plot. Correlation was statistically significant (see Table 3.3).

Using all the recorded variables to predict factors that determine the density of rat burrows in a general linear model (GLM) revealed a significant positive effect of the number of large-seeded trees per plot (p = 0.007; Table 3.4). Despite the gentle gradient (0.136), the positive relationship was also shown in the lower standard error (red lines in Figure 3.6).

Table 0.4: Results of the best model for the factors predicting the density of burrows in NNFR (Density of burrows (m^{-2}) = number of large-seeded trees per 400 m^2 plot + tree diversity. $F_{2, 47}$ = 5.24, R^2 = 0.15. The starting model which had all variables with their possible interactions had an AIC of 113, but the best model had an AIC value of 99.

Variable	**Estimate**	**Standard error**	**t value**	**p value**
Intercept	1.668	0.732	2.28	0.027*
Number of large-seeded trees	0.136	0.049	2.798	0.007**
Tree diversity	-0.7	0.372	-1.881	0.661

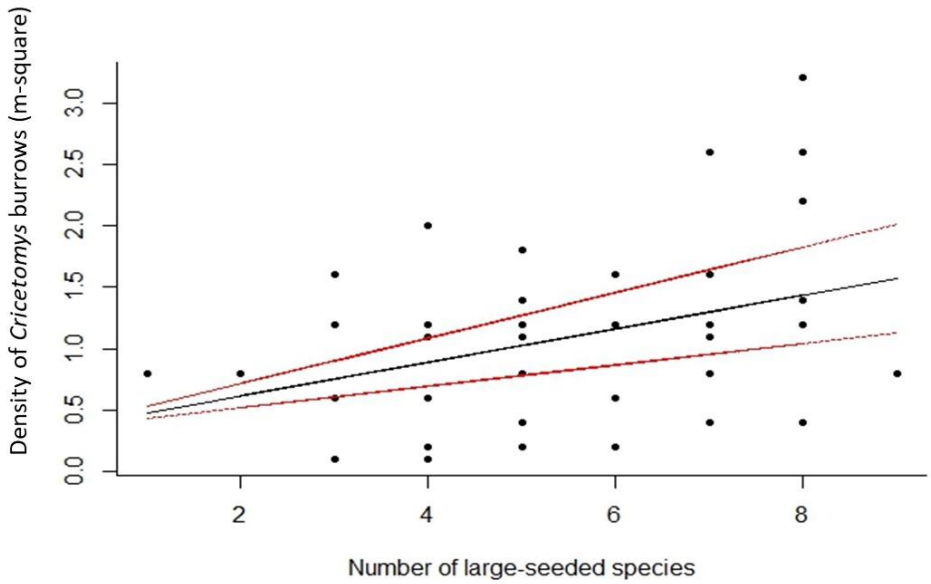

Figure 0.6: The predicted relationship between the number of large-seeded species and the density of *Cricetomys* burrows in small plots (400 m^2) based on the model results in Table 3.4. Each point represents burrow density in a small plot. Mean regression estimate is shown in black line while red lines below and above the black lines represent lower and higher standard errors respectively.

3.4 Discussion

Similar to many other studies (e.g. Cid *et al*., 2013; Emsens *et al*., 2013; Jorge & Peres, 2005; Silvius & Fragoso, 2003), which found that scatterhoarding rodents occurred at higher densities in areas with abundant large-seeded tree species, this study has also showed that an increasing density of large-seeded tree species was positively related to the density of *Cricetomys* burrows in small plots. Although the direct density estimates of *Cricetomys* were not higher in forest sites with more abundant large-seeded species, there were more *Cricetomys* burrows in areas with abundant large-seeded species.

3.4.1 *Cricetomys* abundance and distribution of trees

If the density of *Cricetomys* was higher in areas with abundant large-seeded trees, then more photographs of the rats would have been captured by the camera traps in such areas than in areas were large-seeded species were less abundant. This was

however, not the case. Even though using occupancy models with my photographic data may have provided different estimated densities, the trend would still be similar to my results because of the trap rate. I found that the direct abundance of *Cricetomys* was not significantly related to the abundance of large-seeded trees. I propose two possible explanations for my findings: i) possible home range extensions, and ii) possible short-range seasonal migration. Firstly, the fruiting phenology of large-seeded trees during the period of this study (September to November) explains the possible extended movements of the rats beyond their normal home ranges. Because most tropical trees fruit during the major rainy seasons (Heideman, 1989; Smythe, 1970; Sun *et al*., 1996), the beginning of the dry season is often a period of food scarcity (Foster, 1982; Smythe, 1970; Terborgh, 1983). In NNFR, a high proportion of community-wide fruiting commonly occurs in the early part of the rainy season, i.e. April, May and June [NMFP Phenology data], while the beginning of the dry season is usually a period of food scarcity. As this study was mostly carried out when fruits were scarce, it is possible that *Cricetomys* carried out more extensive movements from their normal home ranges. Therefore, my estimated density of rats in the large plots may differ if the experiment is repeated in the early part of the rainy season. Due to time constrain, the experiment was not repeated to control for fruiting season. The large plots used in this study may not have been adequately separated from one another (≥ 60 m apart) as the rats have demonstrated the capacity to travel more than a 100 m within their home range (see Chapter 2).

Secondly, it is possible that *Cricetomys* has seasonal shifts in the burrows they occupy; and indeed, individuals have been reported to constantly change burrows (Rosevear, 1969). It would be difficult to relate the densities of *Cricetomys* with associated large-seeded tree species if the tree species are not in their fruiting season and if these rats constantly change burrows. However, from the previous study (Chapter 2) where two large live-trapping grids were set at least 400 m apart in the forest core, no marked individual was trapped in both grids; suggesting that

their possible extended movements and burrow changes may only occur within a limited radius, probably less than 200 m.

Considering the scarcity of fruiting trees during this study, one might expect the density of *Cricetomys* to be higher in forest sites with higher tree diversity, which should potentially hold more alternative food resources. Contrary to this, I found no significant difference in densities of *Cricetomys* within the different large plots that had differing tree diversity. Additionally, I expected the abundance of *Cricetomys* to be related with large plots that had larger trees since such trees often have wider canopies which can provide cover on bright nights and reduce predation risks for the rats. However, I found that the abundance of *Cricetomys* was not directly related to an abundance of trees that had large canopies.

While the densities of large-seeded trees have been shown to be positively related with the actual densities of scatter-hoarding rodents in the Neotropics (Aliaga-Rossel *et al*., 2008; Emsens *et al*., 2013; Jorge & Peres, 2005), my study did not support this trend. One important point to note is that my remote-sensing method of density estimation may not be as reliable as the line transect method used by Jorge and Peres (2005). However, given the nocturnal activity pattern of *Cricetomys*, the camera-trapping was the best non-invasive option.

3.4.2 Density of *Cricetomys* burrows and distribution of trees

The positive correlation between the density of *Cricetomys* burrows and the density of large-seeded trees observed in this study supports the idea that small mammals are more abundant in areas where their food sources are also abundant (Jorge and Peres, 2005). To ensure their continuous survival in areas with abundant food resources, small mammals may utilise most of the refuges available within their home ranges (Aliaga-Rossel et al., 2008). Abundant refuges of small mammals may be observed in areas where the animals occur at higher densities. For rodents, which nest and take refuge in burrows, it is advantageous to make burrows in areas that hold abundant food resources. The positive relationship between the number of large-seeded trees and the density of burrows in this study suggests that

Cricetomys densities will be higher in forest sites that hold abundant large-seeded trees.

While it is possible that a high density of burrows may simply represent an abundance of burrow exits of a few individuals, it is important to note that it may not necessarily be the case with *Cricetomys*. Ajayi (1997) excavated 45 burrows of *C. gambianus* and found that half of them had only one burrow exit and that the highest number of exits per burrow was four. Additionally, the maximum burrow length of about 3 m reported by Ajayi (1977) suggests that my burrow density estimates are reliable since the microsites that I surveyed for burrows were at least 5 m apart in each small plot. However, it is not known whether an individual rat or monogamous pair can dig more than one burrow within their home range as more burrows are likely to provide quick escape routes from predators.

It has been demonstrated that higher densities of scatterhoarding rodents occur in areas with stands of a preferred tree species. For example, Aliaga-Rossel *et al*. (2008) showed that the Central American agouti (*D. punctata*) occurred at a higher density in forest sites with abundant *Astrocaryum standleyanum* trees compared with other large-seeded trees. Similarly, the red-rumped agouti (*D. leporina*) has been shown occur at higher densities under high-density natural stands of *B. excelsa* trees. *Carapa oreophila* trees, which produce large seeds that serve as favourable food sources for *Cricetomys* (pers. obs.) were not observed to disproportionately occur in different patches of the forest within the CTFS-ForestGEO plot in NNFR (see Appendix 3.1). This might have offered more insight into the relationship between *Cricetomys* and a favourite large-seeded tree species. Although this study did not target only one or a few large-seeded tree species, the results suggest that *Cricetomys* densities are higher at forest sites with more large-seeded tree species. Given the paucity of fruit resources in montane forests compared to lowland forests (Chapman *et al*., 2016), it is unlikely, that *Cricetomys* will prefer to burrow in areas where only a single large-seeded species occurs.

Factors that determine the density of *Cricetomys* burrows as examined in this study are by no means exhaustive. Other possible factors like the physical and chemical properties of the soil, arthropod abundance and temperature may affect the locations and densities of *Cricetomys* burrows. However, these factors are yet to be explored in NNFR.

3.4.3 Implications for seed dispersal

If *Cricetomys* exclusively cache large seeds within their home ranges, then it is likely that the clumped distribution of large-seeded trees will persist within the forest. Since the burrows observed in this study were associated with mixtures of tree species, it is unlikely that *Cricetomys* will preferentially make their burrows under only one large-seeded tree species. Hence, the clumped distribution of large-seeded trees may persist as species clusters. However, it may be disadvantageous for *Cricetomys* to cache seeds in their home ranges when they occur in areas where the density of their conspecifics is high because the stored seeds may be easily found by other individuals. In this case, it may pay to scatterhoard seeds outside of the home range. If *Cricetomys* moves seeds longer distances to hide them away from conspecifics, then cached seeds may have a higher chance of escaping post-dispersal predation, and thus a high conspecific density of the rats may inadvertently become advantageous for dispersal of large-seeded species. In the long term, this can help sustain tropical tree diversity within such forests.

3.4.4 Conclusion

In conclusion, this study has shown that higher densities of *Cricetomys* most probably occur in forest sites with abundant large-seeded species, but that tree diversity and size have no apparent effect on the density of *Cricetomys*.

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Chapter 4: Effect of predation risk on microhabitat use by African giant pouched rats (*Cricetomys* sp. nov) in Nigeria

Abstract

How rodents perceive predation risk can alter their seed foraging behaviour and therefore potentially influence the recruitment of tree species in tropical forests. In this study I used two methods to investigate the effect of predation risk on microhabitat use by the African giant pouched rat (*Cricetomys* sp. nov) in Ngel Nyaki forest, Nigeria. The first method was 'giving up density' (GUD), an index of perceived risk of predation at an artificial food patch, and the second was the

'spool-and-line' approach, whereby unravelling spools are used to trace rodent tracks. Three characteristic microhabitats were used in the GUD experiment: dense understory, open understory and near-burrows. Although lower GUDs were observed close to the rat burrows and in dense understory (safe sites), than in open understory (risky sites), these differences were not significant. Tracking of rat movements using the spool-and-line method also revealed that microhabitat use by these rats mostly depended on the available microhabitats rather than vegetation density/cover. These results suggest that vegetation density had no effect on the perception of predation risk by African giant pouched rats. Consequently, seeds encountered by the rats may potentially be eaten or otherwise dispersed across a wide range of microhabitats within the forest.

4.1 Introduction

For most small animals, predation risk is inevitable. Therefore, such animals adopt predator avoidance or other defensive behaviours that can successfully lengthen their lives (Nonacs & Blumstein, 2010). The manner of predator avoidance varies among species and may include increased vigilance, hiding in safe refuges, increased tendency of fleeing from danger, having a group size that increases efficiency in detecting predators and the production of physical and chemical defences (Edmunds, 1974; Nonacs & Blumstein, 2010).

Although all the predator avoidance strategies employed may be important for reducing the chances of being predated upon, they come at a cost to the prey and there is often a trade-off between the energy and time needed for predator avoidance and other activities (Cowlishaw, 1997; Brown, 1999). For example, an animal spending much time hiding or fleeing, will have little time for foraging. Similarly, an animal that invests heavily in defensive structures may have little energy or time for mate attraction. Nonacs and Blumstein (2010) argued that natural selection acts more on predator avoidance or defence strategy than any other life history trait because predation occurs in all life stages. However, in

contrast, others (Price, et al., 2012; Burin et al., 2016) contend that natural selection acts more on foraging strategies than any other behaviour (Price, et al., 2012; Burin et al., 2016).

To balance the trade-off between foraging and safety, there is need for habitat choice and effective use of the chosen habitats (Cowlishaw, 1997; Valeix et al., 2009). Animals often rely on certain environmental cues to select habitats that support their survival and population growth (Pulliam & Danielson, 1991). For most terrestrial birds and mammals, vegetation structure is important because of its direct or indirect effect on food abundance as well as detection and avoidance of predators (Whelan & Maina, 2005; Abu Baker & Brown, 2010, 2014a; Molokwu et al., 2010; Coleman & Hill, 2014)

4.1.1 **Predation risk and vegetation structure**

Vegetation is a key feature repeatedly associated with predation risk for terrestrial animals (Brown & Kotler, 2004; Andruskiw et al., 2008). Numerous studies have shown that many animals spend more time foraging in, or near habitats with thicker vegetation cover than habitats with sparse or no vegetation (Brown, 2000). These include large herbivores (Kotler et al., 1994; Altendorf et al., 2001; Rieucau et al., 2007; Shrader et al., 2008; Druce et al., 2009; Abu Baker & Brown, 2014b), small rodents (Kotler et al., 1991; Hughes & Ward, 1993; Brown et al., 1998; ; Morris & Davidson, 2000; Mohr et al., 2003) and birds (Oyugi & Brown, 2003; Whelan & Maina, 2005; Molokwu et al., 2010). In most of these studies, predation risk was shown to be the most likely explanation for increased foraging near habitats with thicker vegetation (Brown & Kotler, 2004). Animals often avoid their predators when they carry out their activities close to dense vegetation cover because the probability of being detected and attacked in such habitats is low (Lima & Dill, 1990; Hughes et al., 1994).

Structural differences in vegetation, in terms of successional changes and species composition may affect predation risk for animals. An example is shown in a study by Andruskiw et al. (2008) where predation risk was observed to be higher for red-

backed voles (*Clethrionmys gapperi*) in older, uncut forests compared with regenerating forests in Canada. Conversely, a study by Abu Baker & Brown (2010) in South Africa showed that the four-striped grass mouse (*Rhabdomys pumilio*) perceives a higher predation risk in islands of woody vegetation than in small pockets of fern vegetation in grasslands. However, the extent to which varying degrees of vegetation cover affects animals in tropical African forests is still largely unknown.

Although most animals will require a degree of protection from vegetation to avoid predators, there are some cases where vegetation cover poses more predation risk than open sites. An example is shown in the microhabitat use of two kangaroo rats (*Dipodomys deserti* and *D. merriami*) in California (Bouskila, 1995). These rats significantly utilized the open sites compared with the bushy sites that harboured their major predators—snakes. Similarly, wild guinea pigs (*Cavia aperea*) in Argentina use habitats with shorter grasses that provide them with food and at the same time allow them to scan for predators (Cassini & Galante, 1992).

4.1.2 Measuring predation risk

Predation risk was largely unstudied prior to 1970, when there were almost no measures of predation risk (Beauchamp, 2015). The earliest known work on predation risk (Galton, 1871) suggested that vigilance and gregariousness by Damara cattle (*Bos taurus*) in present day Namibia was due to predator pressure. Although most subsequent studies on vigilance took a similar approach, very few acknowledged Galton's pioneering work (Beauchamp 2015). While vigilance is still widely used as a surrogate for predation risk, it is highly unsuitable for studying nocturnal species and requires considerable effort. Based on the knowledge that avian predators require light to capture their prey at night (Dice, 1945), indices of predation risk were developed for experiments that manipulated light intensity and relative prey abundance or activity (Lockard & Owings, 1974a, 1974b; Thompson, 1982; Kotler, 1984). However, these methods were also difficult to use and had limited application to phylogenetically related species (Prugh & Golden, 2014).

The patch use theory proposed by Brown (1988) has been widely tested and accepted as a means of understanding predation risk (Bedoya-Perez et al., 2013). In this theory, a complete set of costs incurred by an optimal forager before leaving a patch are incorporated in a model; the sum of these costs determines the quitting harvest rate (H) as shown below;

$H = C + P + MOC$

Where *C* = metabolic cost, *P* = cost of predation and *MOC* = missed opportunity costs (other activities an animal could be involved in instead of foraging in that patch). The quitting harvest rate (H) can be determined by a surrogate variable known as the giving-up density (GUD) (Brown, 1988).

Factors affecting animal foraging behaviour in the tropics include temperature, (Bozinovic & Vasquez, 1999), water (Kotler et al., 1998; Molokwu et al., 2010), food availability and breeding (Olsson et al., 2001; Olsson et al., 2002; Molokwu et al., 2008) and predation risk (Lima & Dill, 1990; Brown & Kotler, 2004; Nonacs & Blumstein, 2010). Apart from predation risk, all the other factors can be grouped into missed opportunity costs (*MOC*) or metabolic costs (*C*) as shown in the model above (Molokwu et al., 2008). Although some authors have modified the initial model by adding a third or fourth term which was either the intensity of interference behaviour (*I*), cost of toxins (*T*), benefits of water (*W*), risk of injury (*RI*) or the foraging benefits of information (*FBI*), the basic model still remains more useful except in situations where the added term is controlled for (see Bedoya-Perez et al., 2013 review and the references therein). Despite the difficulty of teasing apart the individual effects of the *C*, *P* and *MOC,* Brown et al. (1994) made a successful attempt for four desert rodent species i.e. Merriam's kangaroo rat (*D. merriami*), the round-tailed ground squirrel (*Spermophilus tereticaudus*), Allenby's gerbil (*Gerbillus andersoni*) and the greater Egyptian sand gerbil (*G. pryamidum*).

By obtaining patch use indices e. g. GUD, field measurements of environmental conditions, and laboratory estimates of *C* and *MOC* for the four species, they

showed that *P* was the major determinant of GUD. Although *P* was variable for the different rodent species, the maximum *P* was greater than 80% for all the rodent species while the minimum *P* was greater than 79% for the two gerbils but for the ground squirrel and the kangaroo rat, minimum *P* was 47% and 52% respectively(Brown et al., 1994). While these results represent *P* for only desert rodents, the general conclusions still apply to most other animal species, as majority of experiments that did not control for *C* and *MOC* often produced similar results (Brown & Kotler, 2004).

Although predation risk in different habitats can inferred from GUD estimates, these inferences can be more informative when additional techniques/indices are involved (Bedoya-Perez et al., 2013). These indices include; animal abundance estimation, activity estimates, behavioural responses, forager identity, growth measurements, handling time, morphological adaptations, mortality estimates, age structure, searching pattern, stress level and habitat use. Obtaining most of these indices in the field is often expensive and labour intensive. However, there are a few cost effective and easier techniques that can be used to supplement GUD methods. One such approach is habitat use experiments using a spool-line-line technique (Strauß et al., 2008) and/or camera traps.

4.1.3 Predation risk in small mammals

Small mammals are the principal group of interest in most GUD studies. Published research using techniques and approaches in conjunction with GUD indicate that small mammals (mostly rodents) occupy more than 70% of the animal taxa studied (see Bedoya-Perez et al., 2013). Reasons which could explain this include their i) propensity to show an obvious response to perceived predation risk, ii) ability to spend more time at food sources and iii) their ability to select habitats (Brown, 1992; Bouskila, 1995; Arcis & Desor, 2003; Apfelbach et al., 2005; Abu Baker & Brown, 2014a; Wasko et al., 2014). Because of the striking similarities in the behaviour and brain function of rodents and humans (Homberg, 2013), rodents often make informed decisions in their foraging behaviour. Additionally, the ability

of rodents to locate food via olfaction, vision and other sensory cues allows them to make unbiased estimates of the resource density in a patch prior to exploitation (Valone & Brown, 1989). Based on their highly efficient foraging strategies, high perception of predation risk and ability to remember rewards, most rodents can be categorised as Bayesian or prescient foragers also known as the 'smarter' and 'smartest' foragers respectively (Brown, 1999; Olsson & Brown, 2006, 2010). Bayesian and prescient foragers are able to make good decisions about the exact time to leave a patch. However, what sets prescient foragers apart is that they have immediate and continuous knowledge about the quality of a food patch (Olsson & Brown, 2010), meaning they can frequently return to a more rewarding patch that has a lower level of risk.

The most recurrent results in the majority of GUD studies involving small mammals show that open microhabitats, farther away from cover usually have higher GUDs while those close to cover (e.g. bush) have lower GUDs (Brown & Kotler, 2004). Apparently, foragers will leave lower GUDs when they are close to safety, which may be near burrows for some rodents e.g. the thirteen-lined squirrel *Spermophilus tridecemlineatus* (Thorson et al., 1998).

While most GUD studies demonstrate the importance of cover in the perception of predation risk by small mammals, a few have identified the effect of spatial variability on GUDs (Bowers & Breland, 1996; Van Der Merwe & Brown, 2008; Abu Baker & Brown, 2010). Using GIS methods in addition to their GUD, Abu Baker & Brown (2010) showed that the perceived predation risk by the four-stripped grass mouse *Rhabdomys pumilio* is lower in large areas that are sparsely covered with woody vegetation than in areas with large clusters of woody plants. Similarly, Van Der Merwe & Brown (2008) demonstrated that perceived predation risk of ground squirrels *Xerus inauris* is lower in areas with fewer burrows than areas where there is a higher concentration of their burrows.

Given the large proportion of GUD studies that have focused on small mammals around the world, it is surprising that tropical rodents are grossly underrepresented

(Menezes et al., 2017). From the few studies carried out in the tropics, it has been demonstrated that the perceived predation risk by small rodents was influenced by the presence of a predator cue (Cremona et al., 2014; Wasko et al., 2014), a light source (Bengsen et al., 2010) and vegetation density (de Arruda Bueno & Motta-Junior, 2015; Menezes et al., 2017). There is however, little or no information on the perception of predation risk by Afrotropical small mammals and this information may be useful in conservation. For example, tropical rodents have been reported as avian nest predators (Hanson et al., 2007; Spanhove et al., 2009a; Spanhove et al., 2009b) and knowledge about their perception of predation risk may be useful in reducing their nest predation effect. Predation risk may have stronger effects on the foraging behaviour of rodents, than removal of top predators and this could potentially alter important ecological processes such as seed dispersal, soil disturbance and predation of invertebrates.

4.1.4 Predation risk, microhabitat use and seed dispersal by African giant pouched rats

The cascading effects of the perception of predation risk and habitat use may have far-reaching implications on community structure (Prugh & Golden, 2014). For example, scatter-hoarding rodents have been shown to exhibit differential seed selection and removal at open and high-cover sites under varying moonlight conditions (Perea et al., 2011). This can potentially determine where seeds will be removed and dispersed in a forest. Considering the dramatic degradation of Afrotropical forest ecosystems (Ahrends et al., 2010; Craigie et al., 2010), Afrotropical scatter-hoarding rodents may be important in bridging seed dispersal gaps but little is known about their behaviour. The African giant pouched rat (*Cricetomys* sp.), being a nocturnal scatter-hoarding rodent is potentially useful in dispersing large-seeded species owing to its large size (Aliyu et al., 2014; Seltzer et al., 2015). Although Rosin & Poulsen (2016) showed that this rat is more of a seed predator and larder hoarder in Afrotropical low land forests, its interaction with large seeds still remains unclear and knowledge about its perceived predation risk and habitat may improve understanding about how these may influence its

dispersal of large seeded species. The aim of this study was to investigate the effect of predation risk on microhabitat use by African giant pouched rats, hereafter referred to as *Cricetomys.*

4.1.5 **Predictions**

This study was based on the following predictions:

i. Despite replenishment of food in a patch, GUDs would be lower from one day to the next, as rats could learn to recognize and remember food locations.
ii. GUDs across forest sites would be the same since *Cricetomys* occur in all forest sites
iii. GUDs in forest sites with abundant large-seeded species would be higher than in forest sites with less abundant large seeded species because *Cricetomys* spend less time foraging in a single patch within forest sites with abundant large-seeded species.
iv. GUDs would be lower in microhabitats with dense understory vegetation because such habitats will potentially provide protection from predators.
v. Microhabitat features in *Cricetomys* paths would differ from the features most commonly available in the surrounding area because rats selectively spend more time in microhabitats that provide protection from predators.
vi. *Cricetomys* would prefer microhabitat features that can potentially aid predator avoidance and food finding.

4.2 Methods

To test my hypotheses, the field study was split into two main parts:

1. Perception of predation risk using GUD (hypotheses i— iv)
2. Habitat use by means of the spool-and line technique (hypotheses v & vi)

4.2.1 **Study site.**

This experiment was carried out in Ngel Nyaki Forest Reserve, Nigeria (see details in Chapter 1). The Ngel Nyaki Smithsonian plot was used for the GUD experiments and is also described in Chapter 2. The locations of the two experiments are shown in Figure 4.1.

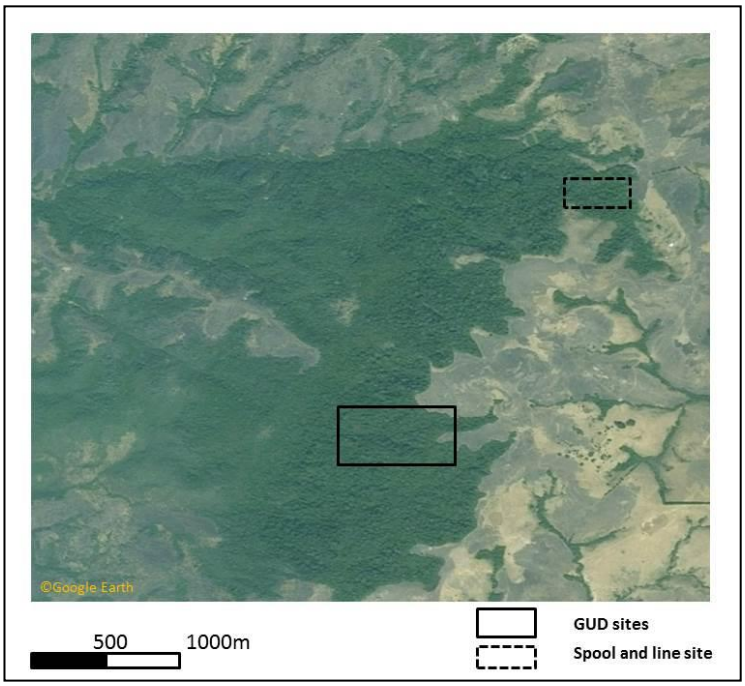

Figure 4.1: Google satellite image of the largest area of continuous forest in Ngel Nyaki Forest Reserve, Nigeria showing sites where the two experiments were carried out.

4.2.2 **GUD experiment**

To estimate the perception of predation risk by *Cricetomys* in the forest I carried out a 'GUD' experiment (Brown, 1988) between the months of September 2016 and September 2017; specifically, in the months of in September-October 2016, February-March 2017, April-May2017 and September 2017. This was carried out within the forested part of the reserve because the study on *Cricetomys* density outlined in chapter 1, showed that the rats rarely visit the grasslands. I used the four sites within the Ngel Nyaki CTFS-ForestGEO plot () as described in Chapter 3. Two of these sites had abundant large-seeded tree species while the other two had few large-seeded tree species. At each of these sites, I categorised microsites into

three types based on understory vegetation and proximity to *Cricetomys* burrows. These microsite categories are i) open microsites — microsites with sparse understory vegetation ('high-risk microsites'), ii) cover microsites — microsites with dense understory vegetation ('low-risk microsites) and iii) burrow microsites — microsites that were close to active burrows ('low-risk microsites'); in most cases these burrow microsites also had sparse understory vegetation (see Figure 4.2).

For each category of microsites at each site, three plastic feeding trays (20cm X 40 cm) were randomly placed such that nearest distance between any two trays was greater than 15 m. On each of these trays, I placed 2 litres of fine gravel collected and sieved from a stream bed within the reserve. Trial experiments with dried seeds of corn (*Zea mays*) and peanuts (*Hypogea arachis*) showed that *Cricetomys* removed more corn than peanut seeds at a ratio of 4:1 (as evidenced from camera trap images and footprints). Hence, corn seeds were used for the experiment. Each experimental session spanned five consecutive days. For the first two sessions, 70 g of corn seeds were mixed with the fine gravel on each tray, this was reduced to 25 in the third session and 20 g in the remaining six sessions. I perforated the plastic feeding trays with tiny holes to allow accumulated rain water to leach out. A daily record of the weight of the remaining corn was obtained by sieving the fine gravel from the large corn seeds. After every measurement of the remaining corn in feeding trays, the mixture was replaced with another quantity as described above for each session. To control for possible moonlight effects, each session were carried out during the dark phase of the moon.

To account for animals other than *Cricetomys* that may visit the traps, three motion triggered camera traps (Bushnell® Trophy cam) was randomly placed close to one feeding tray in each microsite category at all four sites. Additionally, 'Black trakka' paper sheets (Gotcha traps Ltd, New Zealand) were placed around each feeding tray to record footprints of visiting animals.

Figure 4.2: GUD trays kept in 'open' (A), 'cover' (B) and 'near burrow' (C) microsites in NNFR. Cricetomys is also shown harvesting seeds from a GUD tray (D). Yellow circle in (B) shows the location on the GUD tray in cover while the circle in (C) shows the position of an active burrow.

4.2.3 **Spool and line experiment**

To study *Cricetomys* habitat use, I used a spool and line technique (Boonstra & Craine, 1986; Pickett et al., 2005; Strauß et al., 2008). Because this method involves trapping *Cricetomys,* I set out a trapping grid (6 x 4) with a spacing of 30 m for 24 single catch cage traps (61x20.3x20.3cm; reproduced after Havahart®) over 240 trap nights (24 traps x 10 nights). Since *Cricetomys* are most active at night, cages were opened at 1700 h when the sun was setting and the traps were checked and closed by midnight. For each trapped rat, records of sex, body length and trap location were noted. Each trapped rat was uniquely marked in its subcutaneous dorsal region with a passive integrated transponder tags (Tierchip® sterile Iso-compliant microchip with implantation device ISO-Transponder 1.4 x 8.5 mm IG) before gluing ~ 200 m cotton spool (enclosed in a heat shrink wrap) on its flank with an epoxy resin glue (Epoxy steel gum® TCM, Taiwan technology). The thread from the anterior

end of each spool was pulled and tied to the nearest sapling before releasing the trapped rat: as the rat moves, the rest of the thread unwinds, leaving behind a trail of the rat's track. The marking and release of each rat was done at the location where it was trapped.

The next morning, ignoring the first 20 m of the unwound thread, which was the assumed flight response of the rat, the rat's track was traced by following the rest of the unwound thread trail. Microhabitat variables were recorded in a 1 m^2 quadrat at the centre of every 6 m of the trail. These variables included estimated percentages of exposed ground (with no vegetation cover) understory density, litter cover and dead logs in six categories (0, 0; 1, 1-20%; 2, 21-40%; 3, 41-60%; 4, 61-80%; 5, 81-100%). Also measured, were the slope and litter depth at each of these points. Additionally, within a 4 m^2 quadrat around the centre of every 6 m of the trail, the number of *Cricetomys* burrows and trees (≥ 10 cm DBH) were recorded. For each of these points, distance to the nearest stream in five categories (1, 0-4 m; 2, 5-9 m; 3, 10-14 m; 4, 15-19 m; 5, ≥ 20 m) was recorded. In order to compare the microhabitats used by *Cricetomys* with unused microhabitats that were available in the immediate vicinity, we created a random trail which originated from the point which the rat was released; this trail had the same length as the rat's trail at each trap location (see Figure 4.3). To ensure complete randomness of the directions in every 12 m of the random trail, we generated random numbers between 0 and 1 using R® software, these numbers where multiplied by 360° to give an angle, which was traced from the north on a compass (Skalski, 1987). The microhabitat variables recorded on the random trail were the same as those measured on the rat's trail.

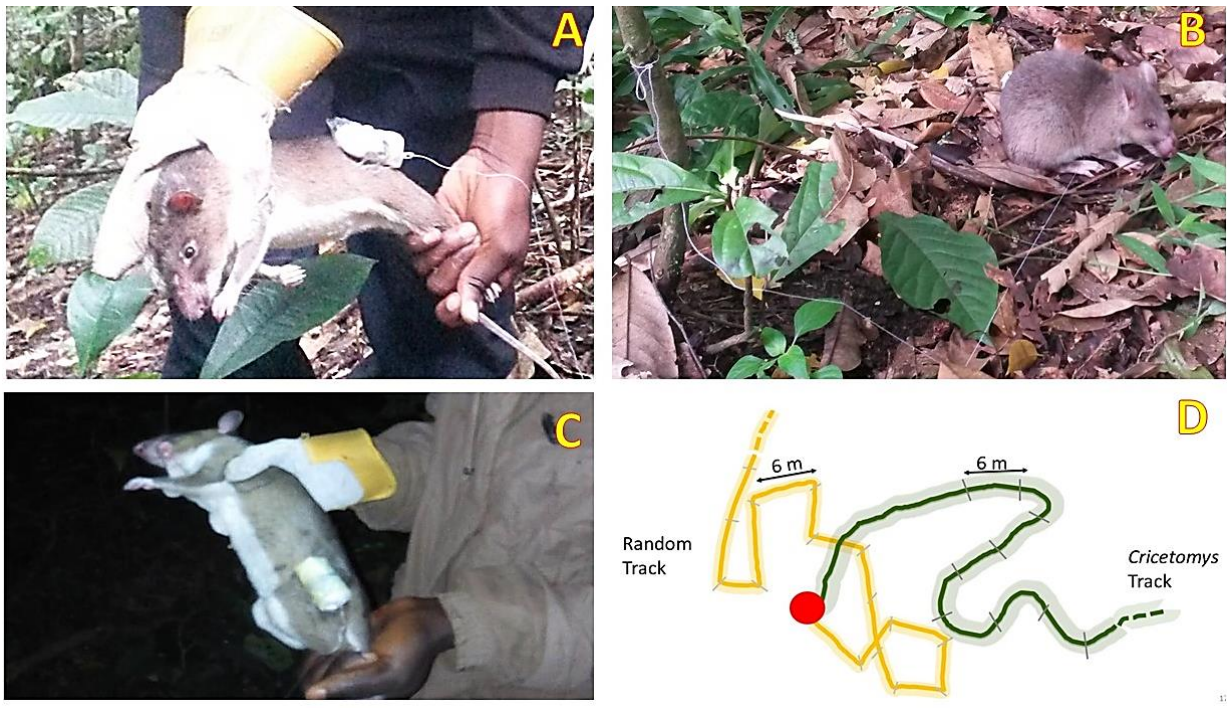

Figure 4.3:Gluing a spool on Cricetomys (A, B and C). One end of the spool is shown tied to a stalk (B). A schematic representation of the *Cricetomys* trail (green lines) and random trail (yellow lines) originating from trap location (red spot) in (D).

4.2.4 **Statistical analyses**

To test for the effect of time, spatial variability and abundance of large-seeded species on *Cricetomys* GUD, I used a general linear model with GUD set as the response variable. A generalised linear mixed effect model in the package 'lme4' in R® (Bates et al., 2017) was used to test for the effect of the microsites (i.e. open, cover and burrows) on *Cricetomys* GUD; observation days, locations within sites, and sites were included as random variables. Since my main objective with the GUD studies was to determine predation risk, I excluded the data from the 4th and 5th observation days from the overall data because they could potentially obscure the results of subsequent analyses.

For all the GUD models, I included the rat densities (directly — camera traps with random encounter model, and indirectly — intensive burrow survey) described in Chapter 2, as explanatory variables. The data were normalized by transforming the

response variable to the power of 0.35 (lambda value), which was obtained from the 'boxcox' function in the package 'MASS' (R core team 2017). Models were checked for violation of model assumptions. Significance of all tests was accepted at $\alpha < 0.05$.

To test for the mean differences in the habitat variables between trails used by the rats and the random trails, I used a student t-test. The relationship between the frequencies of understory density, exposed ground, litter cover and dead log categories (i.e. 0,1,2,3,4,5; see previous section) in the used and random trails were tested using a Spearman's correlation test. In order to compare preferences for microhabitat structures, I used Ivlev's electivity index '*E*' (Ivlev, 1961; Strauß et al., 2008).

4.3 Results

4.3.1 GUD and predation risk

The GUD results show that *Cricetomys* can easily find food sources within their home range. *Cricetomys* were essentially the sole visitors to the feeding trays because the footprints and camera trap images (213 images) were all *Cricetomys* except for three images of an unidentified tiny rat. GUDs were significantly affected by time within a session as GUDs continuously reduced with increase in observation days (see Figure 4.4). The session of the experiment and months had no effect and were removed from the starting model. The final model as shown in Table 4.1 reveals that sites and initial seed quantity had a significant positive effect on GUD. However, the interaction between the initial seed quantity (at 70 g) and observation day had a significant negative effect on GUD, showing that these rats can potentially become habituated to stay longer in a patch with abundant food resources.

Although the GUDs in sites 1 and 2 were lower and not significantly different, the GUDs in sites 3 and 4 which are spatially closer, were significantly higher (see Figure 4.5). The interaction between site and observation day was not significant and was

removed from the starting model. There was no significant effect of the interaction between site and observation day except for site 4 and initial prey density (70 g) (p=0.011) which was negative (see Table 4.2).

Table 4.1: Effect of increasing number of days on GUD. Model: GUD = observation day + site + initial prey density + observation day * Initial seed quantity. Overall adjusted R^2: 0.39, $F_{49,17}$ = 1250

Parameter	Estimates	SE	t-value	p-value	
Intercept	1.93395	0.06641	29.12	< 0.001	***
Day_2	-0.22209	0.0804	-2.762	0.006	**
Day_3	-0.41839	0.07843	-5.334	<0.001	***
Day_4	-0.58673	0.0792	-7.408	<0.001	***
Day_5	-0.59174	0.07887	-7.503	<0.001	***
Site_2	0.06963	0.06377	1.092	0.275	
Site_3	0.33824	0.062	5.456	<0.001	***
Site_4	0.3468	0.06172	5.619	<0.001	***
Initial seed quantity 25g	0.40821	0.14327	2.849	0.004	**
Initial seed quantity 70g	1.88041	0.11573	16.248	<0.001	***
Day_2: Initial seed quantity 25g	0.20947	0.20649	1.014	0.311	
Day_3: Initial seed quantity 25g	0.42744	0.2447	1.747	0.081	.
Day_4: Initial seed quantity 25g	0.23487	0.24494	0.959	0.338	
Day_5: Initial seed quantity 25g	-0.4272	0.24491	-1.744	0.081	.
Day_2: Initial seed quantity 70g	-0.25931	0.17677	-1.467	0.143	
Day_3: Initial seed quantity 70g	-1.00337	0.18099	-5.544	<0.001	***
Day_4: Initial seed quantity 70g	-1.24797	0.18953	-6.584	<0.001	***
Day_5: Initial seed quantity 70g	-1.67317	0.2007	-8.337	<0.001	***

Significant p values are denoted by asterisk (*): ***, <0.001; **, >0.001<0.01; *,>0.0 1<0.05

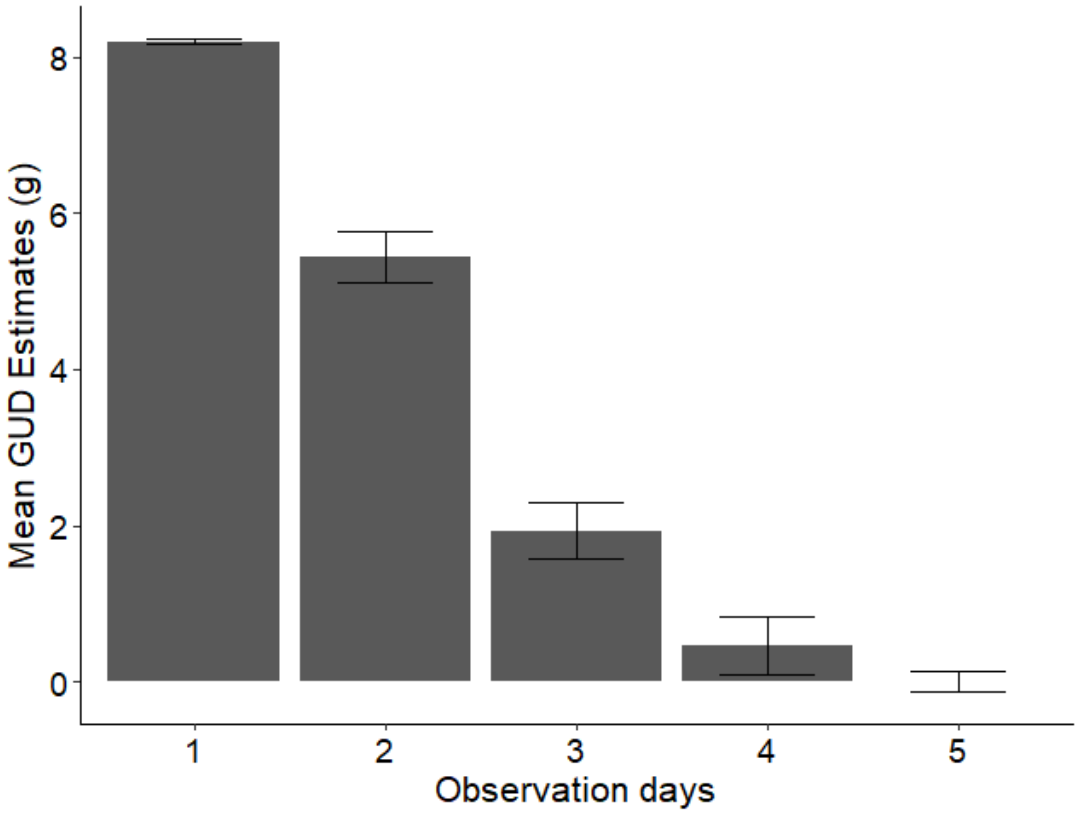

Figure 4.4: GUDs in the five consecutive days within a session. GUDs increasingly become lower as the number of days increased.

Table 4.2: Effect of site on GUD. Model: GUD = site + initial prey density + observation day + microhabitat+ observation day * Initial prey density + site : microhabitat , overall adjusted R^2: 0.41, $F_{22,25}$ = 775

Parameter	Estimate	SE	t-value	p-value	
Intercept	1.569	0.068	23.116	< 2e-16	***
Site_2	0.111	0.090	1.226	0.221	
Site_3	0.175	0.087	2.002	0.046	*
Site_4	0.228	0.088	2.599	0.010	**
Initial seed quantity 25g	0.157	0.133	1.181	0.238	
Initial seed quantity 70g	1.109	0.110	10.080	< 2e-16	***
Day_2	-0.143	0.050	-2.881	0.004	**
Day_3	-0.268	0.048	-5.532	0.000	***
Burrow	0.051	0.088	0.579	0.563	
Open	0.093	0.084	1.115	0.265	
Site_2 : Initial seed quantity 25g	0.193	0.162	1.194	0.233	
Site_3 : Initial seed quantity 25g	0.118	0.161	0.734	0.463	
Site_4 : Initial seed quantity 25g	0.051	0.163	0.315	0.753	
Site_2 : Initial seed quantity 70g	0.214	0.134	1.594	0.111	
Site_3 : Initial seed quantity 70g	0.056	0.132	0.423	0.673	
Site_4 : Initial seed quantity 70g	-0.326	0.128	-2.548	0.011	*
Day_2 : Initial seed quantity 25g	0.128	0.128	1.003	0.316	
Day_2 : Initial seed quantity 70g	-0.182	0.110	-1.657	0.098	.
Day_3 : Initial seed quantity 25g	0.295	0.152	1.944	0.052	.
Day_3 : Initial seed quantity 70g	-0.552	0.112	-4.920	0.000	***
Site_2 : burrow	-0.134	0.123	-1.085	0.278	
Site_3 : burrow	-0.109	0.120	-0.904	0.366	
Site_4 : burrow	-0.004	0.120	-0.030	0.976	
Site_2 : open	-0.247	0.120	-2.050	0.041	*
Site_3 : open	0.064	0.117	0.544	0.586	
Site_4 : open	0.169	0.116	1.454	0.146	

Significant p values are denoted by asterisks (*): ***, <0.001; **,>0.001<0.01, *,>0.

01<0.05

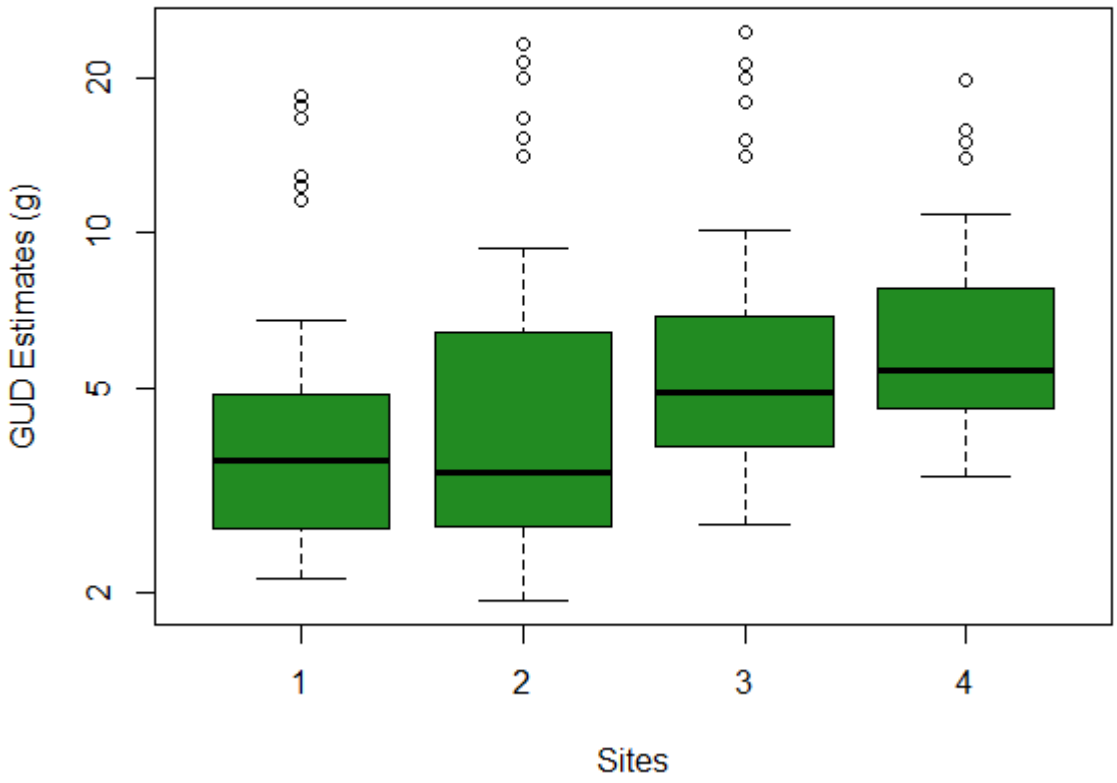

Figure 4.5: Box plot showing log scaled GUD estimates in the four different sites. The 25th, 50th and 75th percentiles are shown by the lower halves, middle lines and the upper halves of the boxes in the plot while the whiskers represent the 5th and 95th percentiles of the data.

Considering the effect of sites with abundant large-seeded tree species, sites 1 and 4 were grouped together as the abundant sites while sites 2 and 3 were grouped as the less abundant sites. A t-test used to compare the two groups showed no significant difference ($p = 0.91$) between the two means which were 6.58 g for the less abundant and 6.62 g for the more abundant sites; Figure 4.6 illustrates the data.

There was no effect of microhabitats on *Cricetomys* GUDs as revealed by the best linear mixed effect model (see Table 4.3), although that same model showed a significant effect of the initial prey densities and the mean densities of burrows per

site. Although the GUD estimates in the open were higher than in other microhabitats within the three, different initial seed quantity categories (i.e. 20 g, 25 g and 70 g), this difference was not significant (see Figure 4.7).

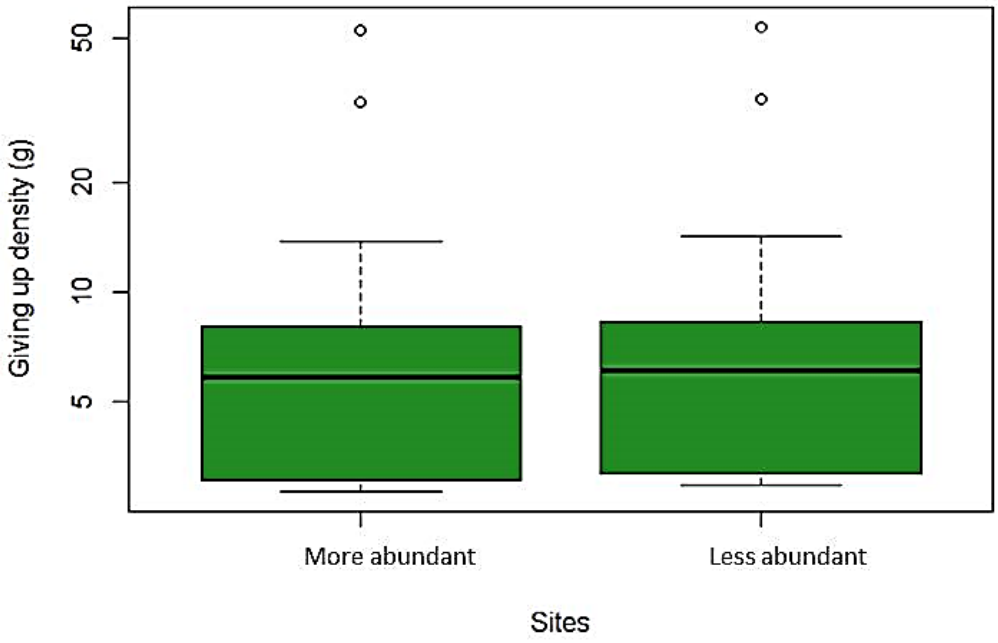

Figure 4.6: Box plot showing log scaled GUD estimates at sites with abundant and less abundant large-seeded species. The 25th, 50th and 75th percentiles are shown by the lower halves, middle lines and the upper halves of the boxes in the plot while the whiskers represent the 5th and 95th percentiles of the data**.**

Table 4.3: Effect of microsites, initial seed mass and mean number of burrows on the GUD. (R-square = 0.51. AIC: from 7554.48 to 6326

Parameter	**Estimate**	**SE**	**df**	**t-value**	**p-value**	
Intercept	12.312	2.839	3.8	4.337	0.01351	*
Burrow	-1.069	1.09	793	-0.981	0.32689	
Open	1.547	1.073	793	1.442	0.14973	
Initial seed quantity 25g	6.573	1.459	793.4	4.505	7.63E-06	***
Initial seed quantity 70g	35.223	1.181	793.2	29.832	< 2e-16	***
Mean number of burrows per site	-15.608	5.953	793	-2.622	0.00891	**

Significant p values are denoted by asterisks (*): ***, <0.001; **,>0.001<0.01; *,>0.01<0.05

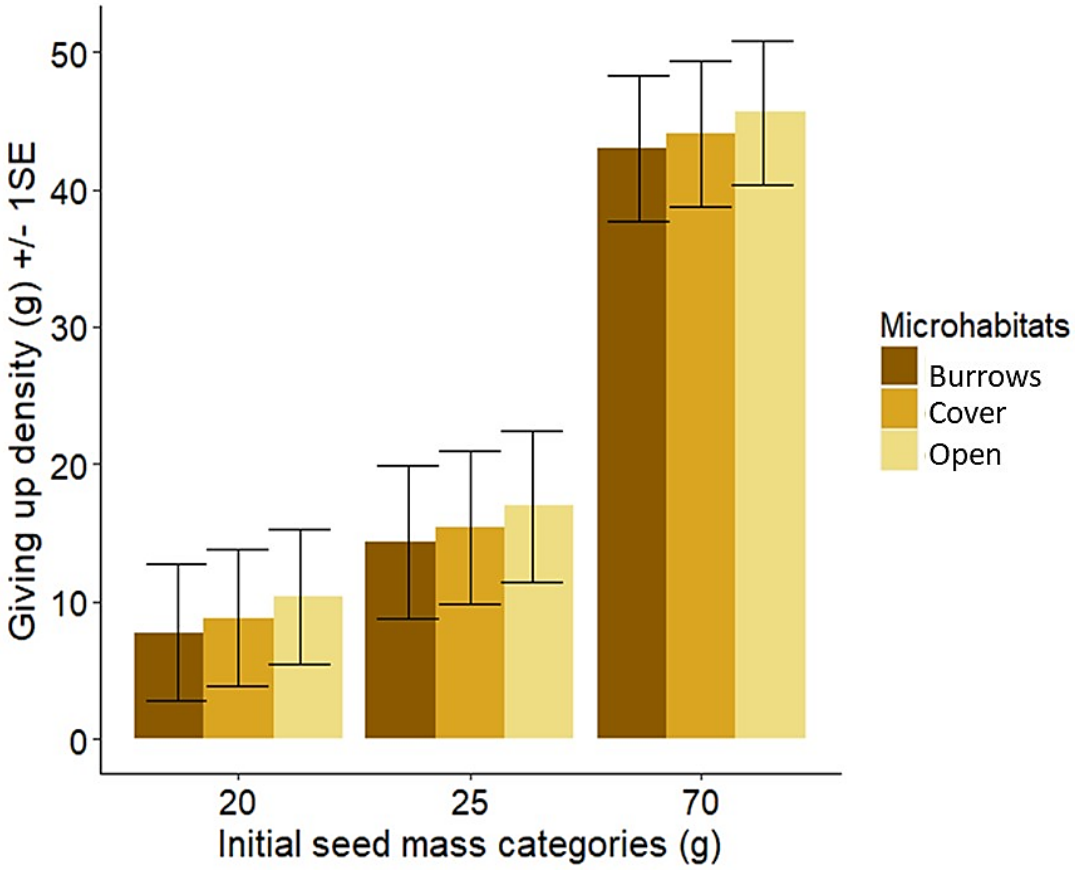

Figure 4.7: Effect of initial prey density on GUD density of *Cricetomys*. Pairwise differences between the microhabitats are not significant ($p \geq 0.05$).

4.3.2 **Microhabitat use**

Of the 17 rats that were caught and fitted with spools, 15 made tracks greater than the assumed 20 m flight response distance. Distances along the unwound spools ranged between 24 m and 144 m, with a mean of 90 ± 6 m.

Comparing the habitat variables between the random sites and sites used by *Cricetomys* in our spool and line experiment showed that understory density, dead

log cover and number of burrows were significantly ($p < 0.05$) higher in the sites used by *Cricetomys* while litter cover was lower (see Table 4.4). The sites used by *Cricetomys* were significantly closer to streams than the random sites. But there was no significant difference in the slope, elevation and number of trees between sites used by *Cricetomys* and random sites.

Table 4.4: Table of T-tests for habitat variables in microsites used by *Cricetomys* and random microsites.

Parameter	**Estimate (*Cricetomys*)**	**Estimate (Random)**	**t-value**	**df**	**p-value**	
Slope	17.39	17.91	-0.828	450.99	0.4081	
understory density	2.193	1.891	2.541	450.97	0.011	*
litter cover	2.784	3.099	-3.198	441.98	0.002	**
dead log cover	0.637	0.443	2.5488	440.07	0.011	*
litter depth	2.05	2.161	-1.104	447.75	0.2701	
number of burrows	0.262	0.149	2.312	422.74	0.0211	*
number of trees	0.505	0.455	0.804	399.55	0.4217	
distance to nearest water	3.965	4.552	-4.737	397.33	<0.001	***
Elevation	1565.54	1587.63	-2.27	236.45	0.023	

Significant p values are denoted by asterisks (*): ***, <0.001; **,>0.001<0.01, *,>0.01<0.05

Spearman's correlation test revealed a positive relationship between the frequencies of the used and random habitat variables recorded i.e. understory density, exposed ground, litter cover and dead logs (Table 4.5). This indicated that the rats used all available microhabitats within their home ranges; Figures 4.8-4.11 illustrates the data.

Table 4.5: Correlation between *Cricetomys* used and random habitat variables. LCL and UCL refers to lower confidence limits and upper confidence limits respectively.

Habitat variable	Correlation coefficient	95% LCL	95% UCL	p value	
understory density	0.827	0.046	0.981	0.042	*
exposed ground	0.983	0.849	0.998	<0.001	***
litter cover	0.954	0.627	0.995	0.003	**
dead logs	0.993	0.936	0.999	<0.001	***

Significant p values are denoted by asterisks (*): ***, <0.001; **,>0.001<0.01; *,>0.01<0.05

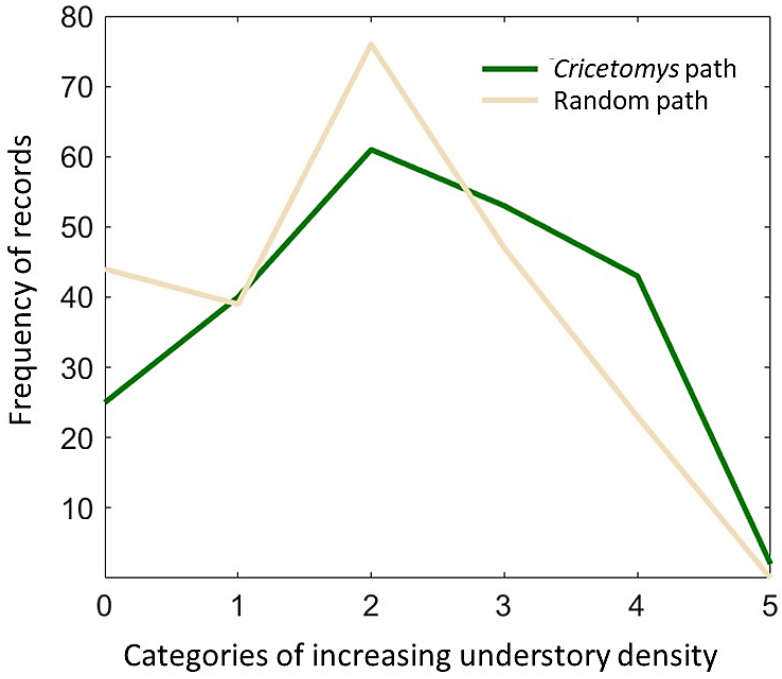

Figure 4.8: Frequencies of the categories of understory density in *Cricetomys* paths and random paths.

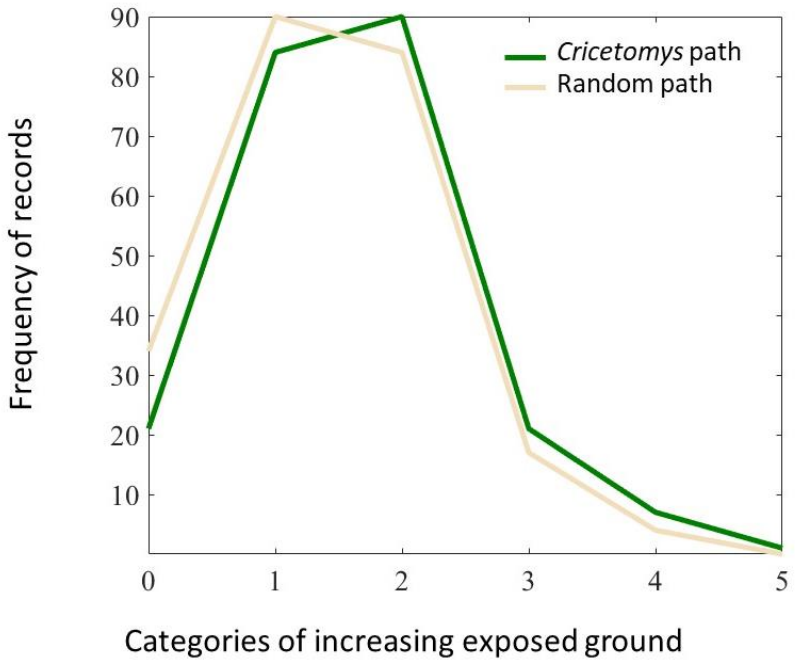

Figure 4.9: Frequencies of the categories of exposed ground in *Cricetomys* paths and random paths.

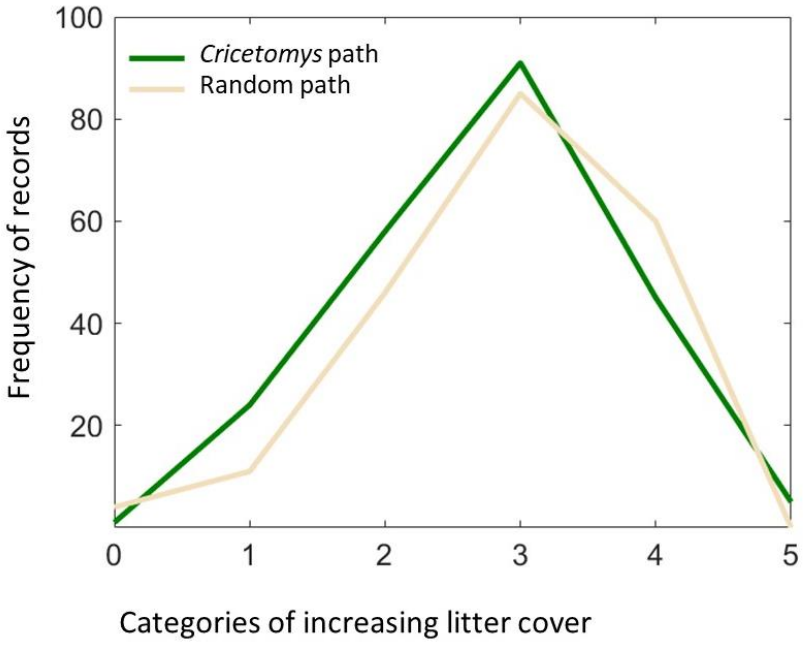

Figure 4.10: Frequencies of the categories of litter cover in *Cricetomys* paths and random paths.

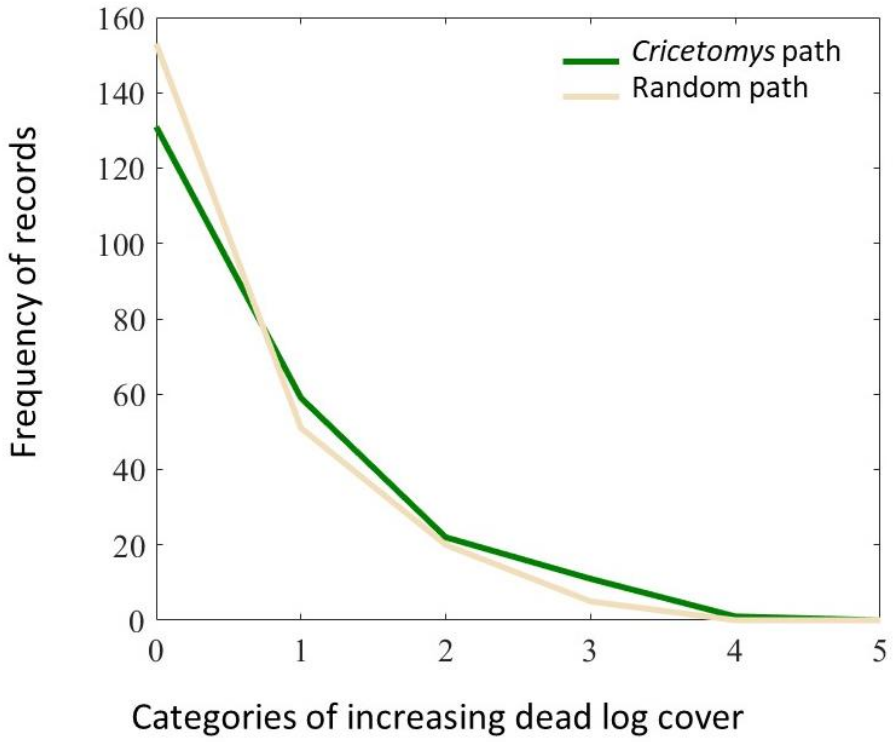

Figure 4.11: Frequencies of the categories dead log cover in *Cricetomys* paths and random paths.

Using the Ivlev's electivity index, this study showed that the rats actively preferred microsites that had more dead logs, more exposed ground and dense understory, but showed a slight tendency to avoid habitats with more litter cover (Figure 4.12) in tropical forests. These preference indices were all ≤ 0.15 which is closer to 0 being the 'no preference' index rather than 1 or -1 which refer to strong active selection or avoidance respectively.

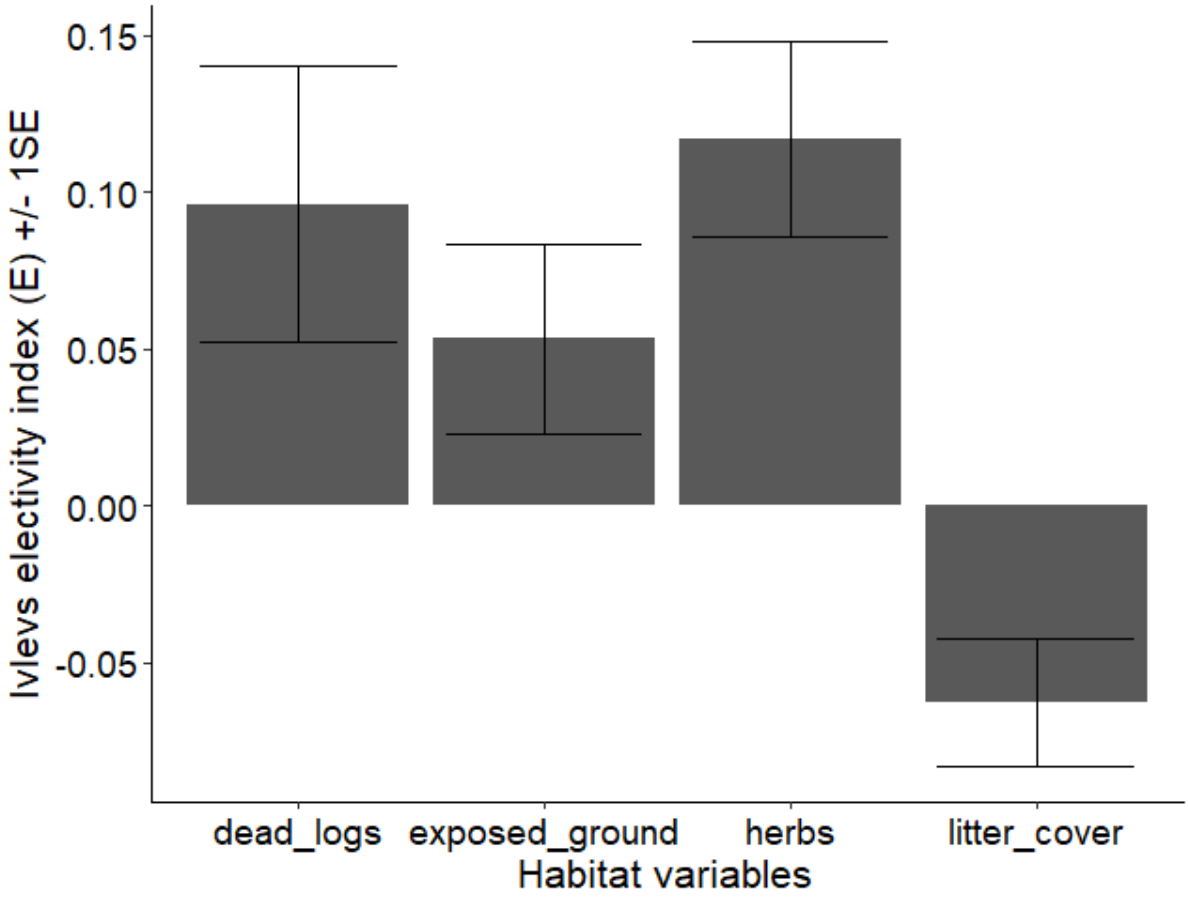

Figure 4.12: Barplot showing preferences for microhabitat variables by *Cricetomys*. Positive values indicate that they were used more often than available while negative values indicate they were use more often than available.

4.4 Discussion

The above results showed that *Cricetomys* had little or no perception of predation risk in the tropical montane forest. Although there was a slight tendency for the rat to frequently use parts of the forest with denser understory vegetation, it equally foraged in open sites, which were generally perceived to be risky for rodents as shown in many similar studies (Hughes & Ward, 1993; Brown et al., 1998; Jacob & Brown, 2000; Morris & Davidson, 2000; Mohr et al., 2003).

4.4.1 **Temporal effect on *Cricetomys* GUD**

The continuous reduction in the amount of food remaining in all the patches following the succeeding experimental nights in the sessions, suggests that *Cricetomys* can easily identify the spatial location of food sources. This also shows that given more time in replenishing food sources, *Cricetomys* learn to either become better at harvesting food or spend more time harvesting without easily giving-up.

Tenacity—being the ability of a forager to show little or no change in its harvest rates when predation risk is increasing (Fraser & Gilliam, 1987), may explain *Cricetomys* foraging in sites that are considered risky for rodents (Brown & Kotler, 2004). Brown & Kotler (2004) suggest three reasons for tenacity in rodents; i) relative invulnerability to predators, ii) poor predator detection abilities ii) behavioural modulation of predation risk e.g. though vigilance and apprehension.

Of these three reasons for tenacity in rodents, *Cricetomys* fits in the first and third. Being relatively larger (~ 1 kg) than most other rodents in the forest, its size may reduce its vulnerability to predators, allowing it to feel safe foraging in habitats that other rodents might perceive as dangerous. But its tenacity may not be attributed to size alone because the Indian crested porcupine (*Hystrix indica*) which is a far heavier rodent (~ 14 kg) still showed a strong sensitivity to predation risk (Brown & Alkon, 1990).

The high olfaction acuity of *Cricetomys* correlates with the functional morphology of its brain (Ibe et al., 2014) and could also contribute to its modulation of predation risk through increased vigilance thus, increasing its preparedness to forage in potentially risky microhabitats. Despite being quadrupedal, the hind limbs of *Cricetomys* have a slight resemblance to those of bipedal rodents in terms of musculature and length; this adaptation for escape may partly be responsible for their frequent utilization of open microsites (Taraborelli et al., 2003).

From the results of my study, it was clear that *Cricetomys* is either a Bayesian ('smarter') or prescient ('smartest') forager since its foraging behaviour conforms with Olsson & Brown's (2010) description of foragers. The consistently low levels of GUD showed that these rats seem to retain information about the location of the feeding trays and searching/detection rates of the corn seeds in the feeding trays. Given the few photographs of possible predators (Chapter 2) which probably indicates paucity of predators, it is likely that *Cricetomys* have learned that already, thus the frequent use of all microhabitat.

4.4.2 **Spatial and habitat variation in perceived predation risk**

Spatial variation in the perception of predation risk may exist as a result of differences in habitat structures (Abu Baker & Brown, 2010). In this study, sites that were relatively closer to the forest edge had higher GUDs than sites that were further into the interior of the forest. This suggests that there may be a large scale spatial effect on either the perception of predation risk by *Cricetomys* or their density distribution. Additionally, forest edges have been demonstrated to have lower food quality and higher risk of predation (Wolf & Batzli, 2004), but this this is yet to be examined in my study site.

4.4.3 **Effect of large-seeded species abundance on *Cricetomys* GUD**

Although I observed no difference in GUDs between areas with abundant large-seeded trees and areas with fewer large-seeded tree species, the effect of large-seeded trees cannot be considered insignificant as I used only two main sites as samples. While the observed spatial difference in GUDs from this study cannot be directly linked with background food sources, it is important to note that fruit production in tropical forests is often seasonal and fruit availability in tropical montane forests is usually lower than in lowland forests (Chapman et al., 2016). Consequently, being able to retain information about the location of food sources may be important for the survival of animals in highland forests. This study suggests that *Cricetomys* sp. nov. easily learns about food sources which may potentially include trees with ripe and falling fruits. Higher GUDs at the start of every session

suggest that these rats do not retain the information of foraging locations for a long period (>3 weeks). However, because experimental sessions lasted for only five days, this could not be ascertained, and it could be that a longer experimental session would enable a longer lasting memory of food sources for these rats.

4.4.4 **Effect of microsites on GUDs**

Although many studies have stressed the importance of covered ('bush' or 'dense vegetation') microsites in the perception of predation risk of many small mammals (see Verdolin, 2006 review and the references therein), my study showed no apparent effect of dense understory (bush) or cover on the perception of predation risk by *Cricetomys*. The consistent slightly higher GUDs in the open microhabitats in this study was not significantly different from GUDs in the bush or burrow microhabitats. This may suggest that there is a higher predation risk in the open microhabitats. However, *Cricetomys* can potentially modulate the risks and still utilize open areas. The consistently lower GUDs at microsites near rat burrows also suggest that the rats feel safer when closer to their burrows than the bushes.

The few GUD studies carried out in the tropics mostly agree with the global pattern at the microhabitat level (Wasko et al., 2014; Menezes et al., 2017). Unfortunately, there are no tropical African GUD studies on rodents, which this study can be compared with and because *Cricetomys* are larger than most tropical African rodents, my results cannot be generalized for other rodents.

4.4.5 **Initial seed quantity and *Cricetomys* abundance**

In this study, the initial seed quantity and the abundance of *Cricetomys* burrows were observed to have the most significant effect on *Cricetomys* GUD. This is surprising because a mere 5 g difference in the initial seed quantity still resulted in a lower GUD. The conventional expectation is that the initial seed quantity may not be important if the animal can hoard or collect food from the patch (Morgan et al., 1997) and so, the GUD should be the same even when the initial seed quantity is different. Although *Cricetomys* often carry excess food to their burrows or caches, they seem to have higher GUDs when the seed quantity is higher.

The abundance of burrows, which is an indirect measure of *Cricetomys* abundance was significant in lowering the GUDs of *Cricetomys*. Though this may partly reflect *Cricetomys* abundance, it is important to note that *Cricetomys* is a lone forager (Ray & Duplantier, 2013). The abundance of rat burrows may however be an indication of *Cricetomys* home ranges that are closer to these sites, thus the few *Cricetomys* foraging in those sites may have good knowledge of resources within their home range and know where to harvest food when available.

4.4.6 **Microhabitat use**

Rats frequently use microhabitats that allow minimum access to predators (Strauß et al., 2008), and this is shown in the frequent use of dense understory vegetation by *Cricetomys* in this study. Although my study showed that *Cricetomys* use all levels of dense understory vegetation, they occurred more frequently at microhabitats with denser understory vegetation. In this study, *Cricetomys* seemed to use all available microhabitats within their small home ranges, which are frequently closer to streams. While *Cricetomy*s rarely used microhabitats with smaller dead logs, there was a less frequent use of microhabitats with large dead trunks of trees because they were not commonly available. *Cricetomys* seem to actively select microhabitats with more understory herbs, exposed ground, and larger dead logs or wood while microhabitats with more leaf litter seem to be slightly avoided. However, the slight habitat preference or avoidance tendencies of *Cricetomys*, as evidenced by the narrow range of Ivlev's electivity values in this study suggest that they do not show a strong preference or avoidance of habitats within their home range.

4.4.7 **Conservation implication**

Considering the seed dispersal behaviour of *Cricetomys* through scatter-hoarding (Aliyu et al., 2014), seeds from large trees which fall into different microhabitats can potentially be located by these rats since they show no apparent sensitivity to predation risk evidenced by their use of most available microhabitats in their home

range. Predation risk may however influence seed dispersal through scatter-hoarding on a larger spatial scale in Ngel Nyaki Forest Reserve.

4.5 Conclusion and recommendation

Overall, this study has shown that predation risk has little or no effect on the foraging behaviour of *Cricetomys* at a microhabitat scale but may be important on a larger spatial scale. It also demonstrates that *Cricetomys* use all the available microhabitats within their home range with slight preference for some microhabitat structures. I recommend that a similar study be carried out in lowland tropical forests in Africa in order to determine the consistency of this behaviour across different forest types.

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Chapter 5: Foraging ecology of African giant pouched rats (*Cricetomys sp*.nov) and African brush-tailed porcupines (*Atherurus africanus*) in Ngel Nyaki forest, Nigeria; removal and fate of large seeds

Abstract

Among the many determinants of seed fate in tropical forests, seed size and nutrient content, in addition to environmental factors have been shown to influence seed removal by rodents. However, how these factors affect scatterhoarding behaviour in African rodents is poorly understood. The current massive decline of large-bodied frugivores in Africa has led to a seed dispersal crisis for large-seeded species, yet little is known about how scatterhoarding rodents interact with these seeds. In this study, I investigated the factors that affect seed removal by two Afrotropical scatterhoarding rodents—*Cricetomys sp*. nov and *Atherurus africanus* and the fate of removed seeds. I used four large-seeded tree species (*Santiria trimera, Beilschmedia mannii, Carapa oreophila* and *Anthonotha noldeae*) and artificial seeds as models. Seeds were marked with the classic thread-tagging technique. I predicted that i) caching frequency will be higher for larger seeds than smaller seeds ii) caching frequency will be higher for nutrient-rich seeds than nutrient-poor seeds iii) larger seeds will be dispersed over longer distances than smaller seeds, iv) seed caching will be more frequent in high-fruit seasons (wet) than low-fruit seasons (dry season). My results showed that the seed caching probability of larger seeds is not greater than smaller seeds. On the other hand, nutrient-rich (high fat content) seeds had a higher probability of being predated, while nutrient-poor (high fibre content) seeds were more prone to being cached. In addition, larger seeds were not moved over longer distances. I also found that the probability of seed caching increased when fruit abundance increased. Although this study demonstrates the high rates of seed predation in Afrotropical forests, it also suggests that a small fraction of seeds can be dispersed by rodents, especially in periods of fruit abundance. Overall, this study reveals that the seed caching

behaviour of scatterhoarding rodents can potentially alter patterns of seed recruitment in an Afromontane forest.

5.1 Introduction

Most tropical forest mammals are either generalist herbivores or omnivores (Fa & Purvis, 1997), often with a high dependence on fruit in their diet. However, because fruit production is seasonal (Ramos Pereira et al., 2010) animals may have to travel long distances in search of food (Dominy et al., 2001) or, if they are territorial, become more efficient at using the resources of a given area (Smith & Reichman, 1984). Efficiency in using an area includes being able to feed on a wide range of species and in some cases, hoarding seeds for later consumption. Animals move seeds away from their natal locations in the process of moving around the forest, or by hoarding them. Through their foraging activities, animals can disperse seeds and contribute to forest diversity (Herrera, 2002).

5.1.1 Animals and seed dispersal

Plant recruitment and the diversity in tropical forests are threatened by the steady decline in large-bodied frugivores (Terborgh et al., 2008). In Africa, 60% of large wild animals were lost from protected areas between 1970 and 2005, with losses up to 85% loss in West Africa (Craigie et al., 2010). This dramatic decline, which involves frugivores such as elephants and large bodied primates is mainly attributable to hunting, habitat degradation and forest fragmentation (Wilkie et al., 2011; Harrison et al., 2013; Camargo-Sanabria et al., 2014) and has resulted in an apparent seed dispersal crisis (McConkey et al., 2012).

Scatterhoarding is a widespread behaviour among small mammals (Forget & Vander Wall, 2001) which involves animals storing food items in depots for later consumption (Vander Wall 1990). Scatterhoarded food items are usually stored in caches; they are randomly hidden under the soil surface or under leaf litter. In tropical forests, rodents are the major group of mammalian scatterhoarders. They

collect seeds from beneath parent plants of from where they have been dropped onto the forest floor by primary dispersers and cache them at varying distances away from source (Morris, 1962; Vander Wall et al., 2005a; Hirsch et al., 2012). However, the extent to which small bodied mammals in Africa act as surrogate dispersers through their scatterhoarding behaviour remains unclear.

5.1.2 **Rodent scatterhoarding and recruitment of tree species**

Plant species can benefit from scatterhoarding through seed dispersal (Forget et al., 2002; Vander Wall 2010). This is because despite the high proportion of seeds that are predated during scatterhoarding, sometimes a sufficient number of seeds survive in their caches so that the advantages of dispersal outweigh the costs of depredation (Jansen et al., 2004; Haugaasen et al., 2010; Jansen et al., 2012). This is especially likely when scatterhoarding rodents are the main or only seed dispersers available, e.g. in the Neotropics where large seeded tree species such as *Astrocaryum standleyanum* (Arecaceae) lost their mutualist megafaunal dispersers during the late Pleistocene and now depend on scatterhoarding rodents for their dispersal (Janzen & Martin, 1982; Guimarães et al., 2008; Jansen et al., 2012).

5.1.3 **Factors influencing scatterhoarding**

Factors influencing rodent behaviour with respect to seed depredation and scatter hoarding include seed and habitat characteristics (Vander Wall, 1990; Forget et al., 1998). Seed traits shown to influence behaviour include seed size, nutritional quality, defensive secondary metabolites (Vander Wall, 1990; Jansen et al., 2002; Wang & Chen, 2009; Yi & Wang 2015) and hardness of seed coat (Yi et al., 2015). Habitat related factors include fruiting season (Hallwachs, 1986; Forget et al., 2002), masting years (Vander Wall, 2002; Hoshizaki & Hulme, 2002; Lichti et al*.,* 2014), availability of alternative food resources (e.g. Forget, 1992; Xiao & Zhang 2016) and animal community interactions (Osunkoya, 1994; Asquith et al., 1997; Li & Zhang, 2007; Wang et al., 2014a; Rosin & Poulsen, 2016a).

5.1.4 **Seed traits**

Two important seed characteristics that influence both seed removal by rodents and the distances to which the seeds are taken are seed size and nutrient content (Wang & Chen, 2009; Vander Wall, 2010; Wang et al., 2013). Larger seeds are usually preferentially removed and taken over longer distances by rodents because seed size is often positively correlated with energy content (Moore et al., 2007; Wang et al., 2012). Using seeds of different species, Xiao et al. (2005), Galetti et al. (2010), Wang et al. (2012), Wang & Ives (2017) showed that species with larger seeds are often carried over longer distances. Still, there is a gap in our knowledge about how seed size affects rodent scatterhoarding behaviour in Africa, and the few studies which report scatterhoarding by rodents (Nyiramana et al., 2011; Aliyu et al., 2014; Rosin & Poulsen, 2016b) have not, so far knowledge, explored seed size selection by controlling for seed type.

Two key nutrients which influence the foraging processes of small mammals are fats and proteins (Lewis et al., 2001; Takahashi & Shimada 2008; Wang & Chen 2012). Seeds with higher protein and fat content should theoretically be preferentially selected by small mammals because these nutrients are needed to compensate for the reduced digestion and assimilation caused by dietary tannins in seeds (Wang & Chen, 2011; Chung-MacCoubrey et al., 1997). Fat content, often used as a proxy for energy content, is an important trait influencing seed removal and dispersal (Xiao et al. 2006; Wang & Chen, 2009). Seed protein content has also been demonstrated to influence foraging preferences of scatterhoarding rodents. For example, Wang and Chen (2012) showed that seeds with higher protein are more likely to be removed and predated upon. Apart from fat and protein content, carbohydrates, which also provide energy might influence seed choice among rodents (Kerly & Erasmus, 1991) and in addition, the non-nutritious crude fibre content in seeds may also affect rodents' choice for seed dispersal. Although other factors such as seed coat hardness may also influence decisions of scatterhoarding rodents in seed removal, their importance is usually secondary relative to seed size and energy content (Wang & Chen, 2009; Yi et al. 2015).

5.1.5 **Retrieval of scatterhoarded seeds**

In most cases, seeds stored in caches by rodents are quickly recovered and either eaten or re-cached in different locations (Vander Wall & Jenkins, 2003; Haugaasen et al. 2010). In some cases, (e.g. Jansen et al., 2002) smaller seeds are recovered and consumed at higher rates than larger seeds. Some scatterhoarding rodents are skilled at retrieving cached seeds, thereby limiting the survival of dispersed seeds (Haugaasen et al., 2010). However, in abundant crop years, seed recovery rates may be lower, thus increasing the survival and chances for establishment of cached seed (Jansen et al., 2004). However, while Jansen et al. (2004) clearly show that the probability of survival of cached seeds increases in abundant crop years, it unclear whether the rates of retrieval of some seed species are higher than others.

5.1.6 **Seasonal fruit availability**

Intra-annual variation in fruit abundance may alter the foraging behaviour and diet of scatterhoarding rodents (Forget et al., 2002; Haugaasen et al., 2010) because rodents need to meet their energy demands in the intermittent periods of food scarcity. Phenological records have shown that fruiting is seasonal in most tropical forests (Ramos Pereira et al., 2010; Wright et al., 1999). Although there are many biotic e.g. (Smythe, 1970) and abiotic factors that determine the fruiting phenology of many tropical tree species, climatic factors such as rainfall are often critical in triggering fruiting of trees (Chapman et al., 2005). While a few studies in the Neotropics have examined the effect of fruiting seasonality on rodents scatterhoarding behaviour (Forget et al., 2002; Haugaasen et al., 2010), it is still unknown whether their results apply to Paleotropical scatter hoarding rodents. One key problem in determining the effect of seasonal resource availability on the behaviour of scatterhoarding rodents is finding a seed species that is available for use across seasons. Although artificial seeds have been used in removal experiments (Forget et al., 2002; Haugaasen et al., 2010; Wang & Chen, 2009; Wang et al., 2014a), there is little or no available data demonstrating their use in the determining effect of seasonal fruit abundance on rodents seed predation/dispersal.

5.1.7 **Scatterhoarding in the Neotropics vs Africa**

In the Neotropics, the contribution to forest regeneration by scatterhoarding rodents is well established (Forget, 1990; Forget et al., 2002; Jansen et al., 2008, 2012; Dracxler & Forget, 2017), among both the smaller rodents (< 250 g) which often tend to be more generalist and to some extent insectivorous in their diet and in larger rodents (>500 g), which are often frugivorous and granivorous (Fleming & Brown, 1975; Vandermeer, 1979; Forget, 1991). However, in Africa, knowledge of the role of scatterhoarding rodents as seed dispersers is still imprecise and requires further studies in both Afromontane and lowland forests (Nyiramana et al., 2011; Aliyu et al., 2014; Rosin & Poulsen, 2016a). This is especially important considering the dramatic loss of large bodied primary seed dispersers (Fa & Brown, 2009; Effiom et al., 2013).

Recently, evidence has emerged, which suggests that the African giant pouched rat (*Cricetomys sp*) and the African brush-tailed porcupine (*Atherurus africanus*) may be the major seed-caching rodents in African forests (Nyiramana et al., 2011; Seltzer et al., 2015; Aliyu et al., 2014; Moupela et al., 2014; Rosin & Poulsen, 2016b). Given their large body sizes and caching behaviour, they may potentially disperse a variety of seeds.

In this study, four different seed species, which varied in size and seed nutrient characteristics were used to investigate seed traits that may determine choice of seed for predation or dispersal by Afrotropical scatterhoarding rodents. In addition, artificial seeds were used to investigate the effect of season in predation/dispersal by rodents. I also asked the question what proportion of visitors to the seeds were the African giant pouched rats, African brush tailed porcupines and other species.

5.1.8 **Predicted**

The research was guided by the following prdictions:

i. The probability of seed caching would be higher for larger seed species as observed in most similar sized neotropical scatterhoarding rodents.

ii. Seed species with higher nutrient reward (fat and protein content) would have a higher probability of being cached as they can potentially provide a greater energetic reward when consumed.

iii. Larger seeds would be dispersed across greater distances as individual rats will prefer to hoard larger, nutrient-rich seeds away from conspecifics.

iv. Larger seeds would have a higher probability of survival as they are dispersed farther away and may be harder for rats to find

v. Smaller seeds would be selected for immediate predation by rats to meet immediate energy demands.

vi. Larger seeds from among seeds of the same species will be cached farther away compared with smaller seeds of the same seed species.

vii. Seed caching frequency would be higher in the wet season, associated with higher fruit production than the dry season which is often associated with lower fruit production.

viii. Seed caching would occur across longer distances in the wet season than in the dry season as most large-seeded tree species fruit in the wet season (Smythe, 1970; Sun et al., 1996; NMFP phenology data).

5.2 Methods

To test the above predictions, the study was split into three parts based on the experiments conducted:

i. Interspecific seed removal experiments (Predictions i to iv)
ii. Intraspecific seed removal experiments and (Predictions v and vi)
iii. Artificial seed experiments (Predictions vii and viii)

5.2.1 **Study Site**

All experiments were carried out between 2014 and 2016 in Ngel Nyaki Forest Reserve (hereafter NNFR) in the Mambilla Plateau, Taraba state, Nigeria (see Figure 5.1). Site description is detailed in Chapter 1.

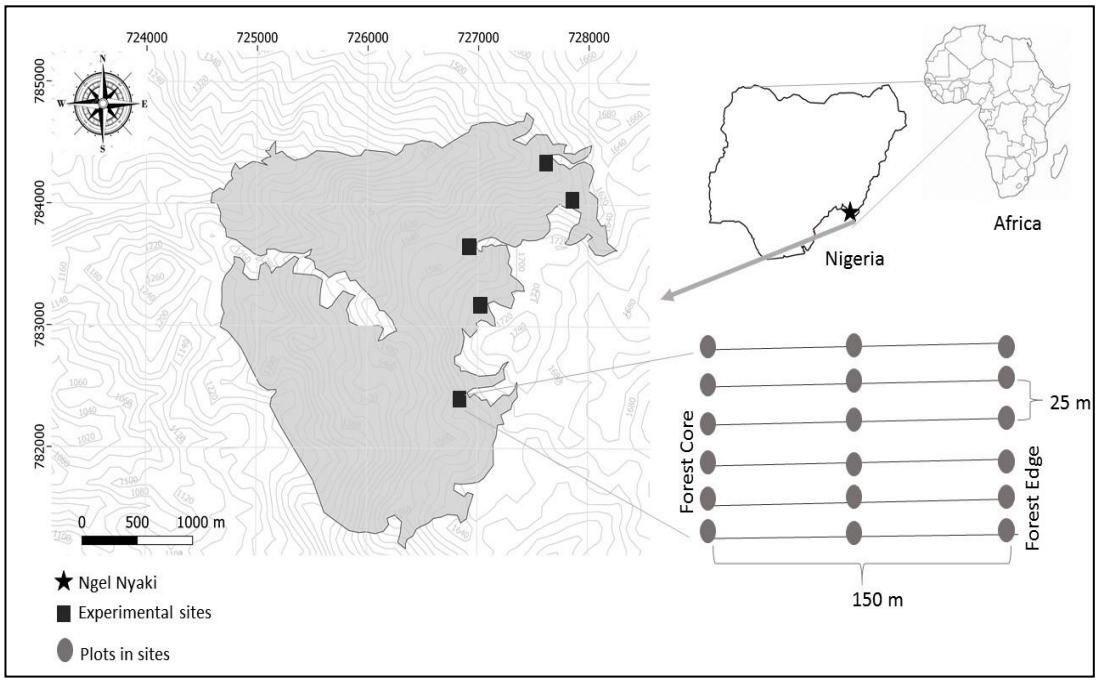

Figure 5.1: Study site showing the elevation map of the main forest patch of NNFR and experimental layout.

5.2.2 **Seed removing rodents in Ngel Nyaki forest**

Recently, two rodent taxa have been found to scatter-hoard seeds in tropical African forests (Figure 5.2), the African giant pouched rats (*Cricetomys spp*) and the African brush tailed porcupine (*Atherurus africanus*) (Nyiramana et al., 2011; Aliyu et al., 2014; Seltzer et al., 2015). These rodents have a relatively large body size (≥ 1 kg) (Kingdon et al., 2013) and actively remove large seeds which can potentially meet their energy demands. *Cricetomys* is a large murid rat, 0.7-0.9 m (n = 53) long (from head to tail) and weighing 0.6-1.2 (n = 53) kg (unpublished data). Previous investigations have shown scatterhoarding behaviour in *Cricetomys* (Aliyu et al., 2014). *Atherurus* is the largest rodent in Africa, measuring 0.3-0.5 m (n = 26) from

head to tail and weighing 0.9-4.2 kg (n = 26) (Emmons, 1983). Scatterhoarding behaviour by *Atherurus* has been recently been demonstrated in Gabon (Rosin & Poulsen, 2016b).

Figure 5.2: Images of *Cricetomys spp* (a) and *Atherurus spp* (b) taken by camera traps at experimental plots in NNFR.

5.2.3 **Interspecific seed removal experiments**

I used seeds of four commonly available species *Anthonotha noladeae, Beilschmedia mannii, Carapa oreophila and Santiria trimera* (Figure 5.3), which varied in seed size and lipid content (see Table 5.1 for seed characteristics). Although the selected seed species varied in size, they were all considered as large seeds because even the smallest (*Santiria*) was longer than my lowest threshold of large seeds (15 mm). I chose 15 mm as the lowest threshold for large seeds based

on the seed size characterization by Smythe (1970) and my prior field trials using smaller seeds i.e. *Leea guineensis* (~5 mm long) and *Zanthoxylum leprieurii* (~3 mm long). From my trial experiments, it was clear that the rodents had a negligible to no interaction with these very small seeds and ants were observed to be the major removers of the small seeds (pers. obs). The large seeds used were collected from at least five different adult trees (for each species) in NNFR. Trees of the chosen seed species occur throughout the forest, although *Anthonotha* is relatively more abundant toward the forest edge.

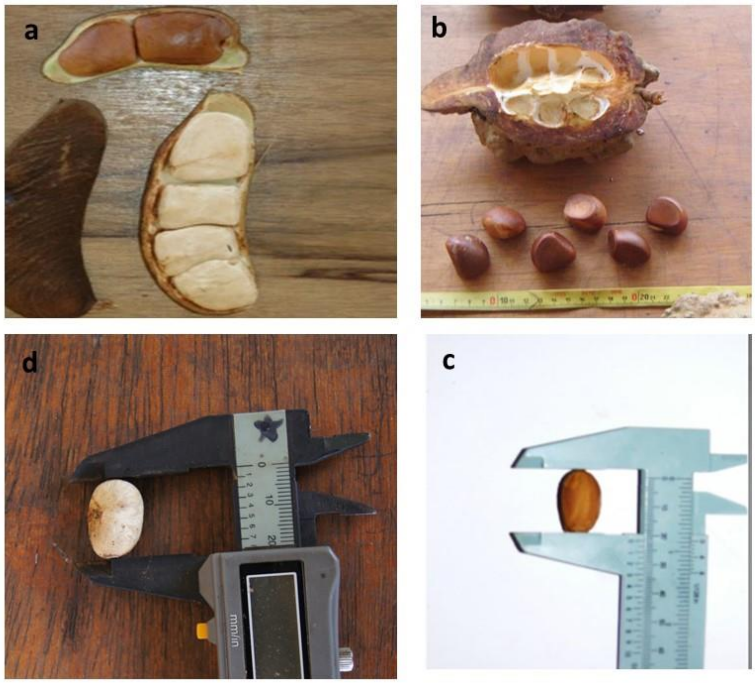

Figure 5.3: Seeds species used for interspecific seed removal experiments. The seeds shown here are *Anthonotha noldeae*, *Carapa oreophila*, *Beilschmedia mannii* and *Santiria trimera*. In a clockwise direction, seeds are shown in order of decreasing size see Table 5.1.

To investigate effect of seed nutrient content on seed predation/dispersal, 20 seed samples of each of the four large-seeded tree species collected in NNFR were chemically analysed for proximate composition of carbohydrates, fats, proteins and fibre (see Appendix 5. 1) at the Chemistry department laboratory of Gombe state University, Nigeria (Table 5.1). Crude protein was determined by the Kjeldahl

method, fibre was determined by ashing, fats by lipid extraction and carbohydrate was determined as remaining content after the subtraction of proteins, fibre and fats (details are shown in Appendix 5. 1).

To investigate seed fate, I sought to determine the probability of a seed being predated or cached. To do this, I set up five sites. Each site was at least 400 m from the nearest site (Figure 5.1). Within each site, I established 18 plots (1 m × 1 m) on six transects which were 25 m apart and 150 m long. The plots were placed at the 0 m (grassland-forest interface), 75 m (forest edge) and, 150 m (forest core) (Figure 5.1). In each plot, I placed ten marked seeds of each species (except 6 seeds of *Beilschmedia* per plot in 2014). The seeds were marked using the classic thread tagging technique (Forget 1990). The seeds were marked by attaching to each seed, a 70 cm long nylon thread through a drilled hole (1 mm in diameter) while the other end of the nylon thread was attached to a pink flagging tape (7 cm) which bore the seed identification details.

Seed fate was observed after the second, fifth and tenth day after seeds were placed on the plots. Removed seeds were searched for within a 25 m radius around each plot and fates of seeds were recorded as either 1) 'predated' when consumed, 2) 'cached' when seed was removed and found buried in the soil or under litter, 3) 'remaining' when seed remained in the plot without being moved, and 4) 'missing' when seeds could not be found. Experiments were carried out when the seed being used were fruiting, thus seeds were not placed in a 'cocktail' fashion. In addition, I randomly stationed at least four motion-triggered camera traps (Bushnell® Trophy cam) at each site. Cameras were checked whenever the seeds in each plot were completely removed or after the tenth day of seed monitoring. Some microhabitat variables within a radius of 10 m around each plot were also recorded; the estimated variables include percentage forest understory cover, percentage litter cover, percentage dead logs and distance to nearest stream. All the dispersed seed from my experiment were monitored every weekly for ~2 months. I recorded signs of seed predation when seeds were no longer in caches and signs of sprouting when apical germination was observed among the cached seeds.

Table 5.1: Characteristics of seed species used in the different experiments from 2014 to 2016. Wet and dry seasons occur only once in a year.

Tree species	Fruiting	Seed size (length x width-mm)	Weight (g)	Fat content (%)	Protein content (%)	Carbo-Hydrate Content %	Fibre content (%)	2014 *Experiment I*	2015 *Experiment i and ii*	2016 *Experiment ii*
Anthonotha noldae	March-May (dry-to-wet)	60.3 x 52.2	36.8	0.22	0.18	26	71	2 forest sites x 6 transects x 3 plots x 10 seeds= 360 seeds	5 forest sites x 6 transects x 3 plots x 10 seeds= 900 seeds— repeated once (1800 seeds) seeds	NA
Beilschmedia mannii	November to February (dry)	26.1 x 11.5	4	1.26	1.15	37	31	3 forest sites x 4 transects x 3 plots x 6 seeds = 216 seeds	4 forest sites x 6 transects x 3 plots x 10 seeds = 720 seeds	NA
Carapa oreophila	June-October (late wet)	38.3 x 31	21.9	12.5	0.73	56.68	1.97	5 forest sites x 6 transects x 3 plots x 10 seeds = 900 x 2 reps =1800 seeds	Idem 2014 with no reps (900 seeds)	4 forest sites x 6 transects x 3 plots x 10 seeds = 720 seeds.
Santiria trimera	April to June (early wet)	21.4 x 16.1	2	4.6	11.1	48.8	15.9	5 forest sites x 6 transects x 3 plots x 10 seeds= 900 seeds	NA	NA

5.2.4 **Intraspecific seed removal experiments**

In this study, I used *Carapa oreophila* (Meliaceae), a species with widely variable seed sizes (Figure 5.4) to examine the effect of seed size on rodents' choice of seeds for predation and dispersal. *Carapa oreophila* (Meliaceae) (Kenfack, 2011) is a common small tree within NNFR. It reaches 12 m in height but is most noticeable for its large fruit with diameter ranging from (10-15 x 7-12 cm) and produced throughout the year but most abundant towards the end of the wet season between August and October. Within each fruit, there are up to 16 seeds, which show a 20-fold variation in size; the size of seeds used in my study ranged from 16 – 61 mm long and weighed between 0.88 – 46.1 g; the mean (± SD) size of the seeds was 38.3 (± 5.6) mm long, 31.0 (± 5.7) mm wide and 21.9 (6.0) g in weight (n = 40).

Using the same experimental design as in the first experiment above (4.3.3), I laid out *Carapa* seeds in 2015 and 2016 (see Table1) and recorded the length and weight of each seed before marking them using the thread-tag marking technique (Forget 1990). In addition, I randomly stationed at least four motioned triggered camera traps (Bushnell® Trophy cam) at each site. Microhabitat variables, which included litter depth, estimated herb density, distance to nearest stream, slope and percentage dead logs within a radius of 10 m around each plot, were also recorded.

Figure 5.4: *Carapa oreophila* seeds have a wide variation in length and mass. The individual seeds shown here only illustrate the differences, they are not the two extremes measured in this study.

5.2.5 **Artificial seed experiments**

The effect of seasonal variation in fruit availability on seed predation/ dispersal was examined through seed removal experiments using artificial seeds placed in 12 forest sites; these sites were different from the sites where experiments using actual seeds were conducted. The experiment was carried out monthly in the dry season (February and March) and the wet season (June and August) of 2016. Due to logistic reasons, the experiment was not carried out in the months between the wet and the dry season i.e. at the beginning and end of the wet season.

5.2.5.1 Preparation of artificial seeds

Artificial seeds were prepared using laterite and peanuts (*Arachis hypogea*) following the method used in Wang & Chen (2009). The clay and peanut were separately ground in a mortar to obtain fine particles that could pass through a 1 mm mesh. To make artificial seeds with high energy reward, the mixture was made with 70% peanut and 30% soil. Water was added to the mixture until it became doughy; this was then formed into balls that were ~3.5 cm in diameter so that their weights would be ~21g which is the mean weight of the highly favoured *Carapa* seeds. Each artificial seed was connected to a 70 cm nylon thread and a pink flagging tape for ease of identification. The soft balls from the mixture became hard after being dried in the sun (Figure 5.5).

Figure 5.5: Artificial seeds made with peanut flour. Laterite soil being dried on the side and flagging tapes with seed site location for each seed are attached to the artificial seeds with nylon strings.

5.2.5.2 Site selection and experimental design for artificial seeds

This site for this experiment was in the forest interior (> 80m from the forest edge) because previous studies (i.e. Aliyu *et al*., 2014) have shown greater rodent activity in the core than at the edge. Each of the 12 selected sites were at least >100 m apart from the nearest site. The ground litter at each site was lightly cleared in a small area (1m x 1m) in order to place the artificial seeds. For each round of the experiment, 20 artificial seeds per site were placed and observed daily until all the seeds were removed from the plot. Artificial seeds that were consumed were recorded as 'predated' while hoarded seeds were recorded as 'cached' but the seeds that were not found or were severed were recorded as 'missing'.

5.2.6 **Fruit availability**

To account for the effect of food abundance in the experiments above, the relative availability of fruits was considered. Fruit availability which is a proxy for seed availability was estimated using the food availability index method commonly used in the study of primates (Anderson et al., 2002; Sun et al.,

1996) . This method was also applicable in my study because many of the large seeds produced were expected to fall to the ground due to low primate populations and before some large seeds can still be removed from regurgitates and faeces of primates (Dutton et al., 2014). This method basically estimates available food from phenology, tree density and tree basal area data; here, the food availability index was defined as

$$A_m = \sum_{k=1}^{n} D_k B_k P_{km}$$

Where D_k is the density of species k, B_k is the basal area of species k and P_{km} is the percentage of observed trees of species k in a fruiting stage in a month.

I used monthly phenological records from 537 individual trees representing 50 tree species that were relatively common on 17 transects distributed throughout the forest (NMFP Phenology data). Monthly recording of tree phenology data in NNFR has been continuously collected by the Nigerian Montane Forest Project since 2006. The density and basal area of the trees was calculated from a total transect length of 3.6 km (5m wide = 18,000 m^2); this was then extrapolated for the for the major forest patch (7.5 km^2). Seventeen large-seeded tree species were further selected because *Cricetomys* and *Atherurus* had little or no interaction with smaller seeds (≤ 0.5 cm long). A summary of the fruit availability indices for the years 2014 to 2016 are illustrated in Appendix 5. 2. 1a and 5.2.2

5.2.7 **Data analyses**

I included the data from the 2013 pilot study in my data analyses. The probability of caching and predation of the different seed species were analysed in a Bayesian framework using Stan® (Gelman et al., 2015) interfaced with R® (R Core Team 2016). My model considered the hierarchical order of the plots in the transects in each site and other measured habitat variables, to investigate those effects in seed

predation/caching. My posterior probability values were sampled with four chains that converged over 5000 iterations.

In order to investigate the effect of fat content on the probability of seed predation/caching, I used the same Bayesian model as above but this time, categorised seeds into three levels based on their percentage fat content i.e. low (≤1.9%), moderate (> 1.9% <10%) and high (≥10%). Similarly, I categorised seeds into two levels based on their protein content (≤1.9%) low and (≥ 10%) was considered high. Because the percentages of carbohydrates and fibre contents are generally high tropical seeds (Ezeagu 2009), seeds were categorised into three levels based on the percentages of their carbohydrate contents i.e. low (≤10 %), moderate (>10% < 40%) and high (>40%). Categorisation of fibre content was the same as that of the carbohydrate content. A Bayesian logistic regression was used to determine the difference in removal distance among the seed species. For each model, the main effects were considered as significantly different each other when the median credible intervals (difference in credible intervals, DIC) was > 0.05.

A Kaplan-Meier survival analysis was used to investigate seed survival for dispersed seed of the different species. Seed survival was investigated over a period of ten weeks.

I used an overlapping coefficient test OVL (Inman & Bradley, 1989) to determine seed size selection for predation or dispersal. OVL values closer to 1 reveal a completeness of overlap and hence similarities between distributions while values closer to 0 reveal a strong difference between distributions. Using the package *gamm4* (Wood & Scheipl, 2014) in R® (R Core Team, 2016), a generalized additive mixed model (GAMM) was used to test for the effect of seed size on dispersal distance. The fixed effects used in my model included year and smooth functions of seed mass and seed length while sites, lines and plots were entered as random effects in the nested order of the design. All alternative models including other factors had lesser fits.

I used a Bayesian multinomial logistic regression to determine the effect of season and fruit availability on seed fate probabilities. The four seed fates considered as response variables were “cached”, “predated” and “missing” and “remained”. I used a student t-test to compare the distances of removed artificial seeds in the wet and dry seasons. A linear mixed effect model was used to determine the effect season and fruit availability on distance to which seeds were moved to. The sites were set as random variables.

5.3 Results

In all the experiments, the majority of the seeds were removed and predated. Most of the hoarded seeds were singly cached.

5.3.1 **Interspecific seed removal.**

For all the seed species used in the first experiment, a total of 5, 360 (80.0%) individual seeds were removed after 10 days. Of the seed removed, 4,591 (85.7%) seed were predated while 424 (7.9%) seed were cached (see Table 5. 2 for summary of seed removal data).

For all seed species, the probability of being predated when encountered by a rodent was higher than the probability of being cached. Although there were differences among species, these differences were not related to seed size (Figure 5.6). Thus, there was no effect of seed size on seed caching or predation as the seed species did not show a size-based trend of being dispersed or cached. Multiple comparisons however, showed that the probability of being dispersed was significantly higher for *Anthonotha* than the other three species (median DIC ≥ 8%) (Table 5.3). Additionally, probabilities of being predated or cached for *Anthonotha* did not significantly differ between years. *Carapa,* being the second largest seed species on the other hand, had the highest probability of being predated and a multiple comparison of the median posterior distributions showed differences among the species in the following the order

Carapa > *Santiria* > *Anthonotha* > *Beilschmedia*. These differences were all significant (median DIC > 5%) (Table 5.3).

Table 5.2: Seed fate of different large-seeded species in NNFR. Percentages are shown in parentheses.

Species	**Cached**	**Missing**	**Predated**	**Remaining**	**Total**
Anthonotha noldea	240 (11.1)	90 (4.2)	1156 (53.5)	674 (31.2)	2160
Beilschmedia mannii	21 (2.2)	12 (1.3)	390 (41.7)	513 (54.8)	936
Carapa oreophila	114 (4.2)	214 (7.9)	2330 (86.3)	42 (1.6)	2700
Santiria trimera	49 (5.4)	29 (3.2)	715 (79.4)	107 (11.9)	900
Total	424 (6.3)	345 (5.2)	4591 (68.6)	1336 (20.0)	6696

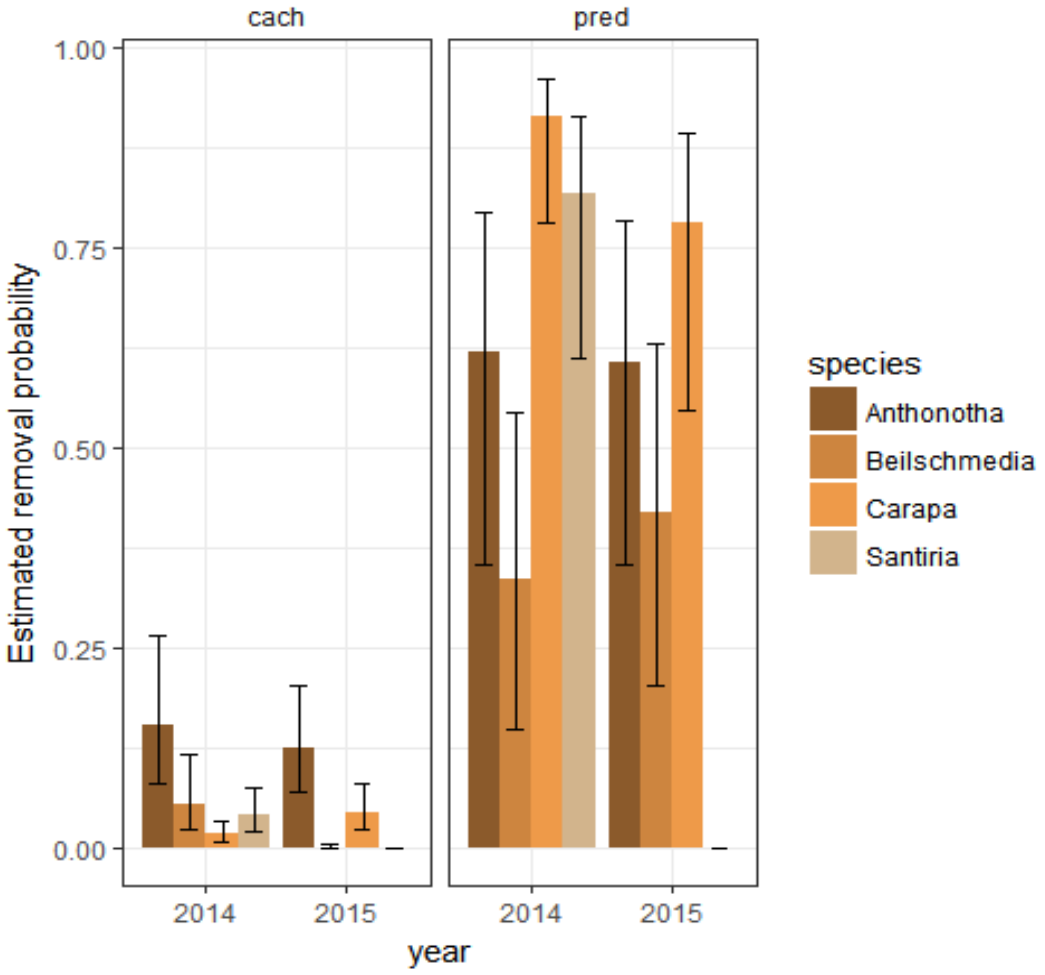

Figure 5.6: Estimated probability of seeds being predated or cached with respect to seed species. Species varied in size in the order *Anthonotha noldeae* > *Carapa oreophila*> *Beilschmedia mannii* > *Santria trimera*, (see Table 1 for details). Probability values were obtained by transforming $(1/(1+e^{(-\beta)})$ posterior distributions from a bayesian binomial logistic regression. Seed fate probabilities were similar across years but different among species. For the average of all years and in all years, *Anthonotha* consistently had a significantly higher probability of being cached than all the other species while *Carapa* consistently had a higher probability of being predated than all the other species. (See Table 5.3 for details on pairwise differences in probabilities).

Table 5.3: Pairwise posterior probability differences of being predated and cached for four (i.e. *Anthonotha*, *Beilschmedia*, *Carapa* and *Santiria*) different seed species in in different years.

Parameter differences	**Predated**				**Cached**			
	Median	**Lcl (2.5%)**	**Ucl (97.5%)**		**Median**	**Lcl (2.5%)**	**Ucl (97.5%)**	
Anthonotha - Carapa | All year average	-0.18	-0.25	-0.11	*	0.11	0.07	0.15	*
Anthonotha - Beilschmedia | All years average	0.23	0.17	0.29	*	0.11	0.07	0.16	*
Anthonotha - Santiria | All years average	-0.31	-0.36	-0.26	*	0.08	0.05	0.12	*
Beilschmedia - Carapa | All years average	-0.41	-0.46	-0.33	*	-0.01	-0.02	0.01	
Beilschmedia - Santiria | All years average	-0.48	-0.53	-0.41	*	-0.03	-0.06	-0.02	
Carapa - Santiria | All years average	0.05	0.01	0.1		0.05	0.03	0.08	
Anthonotha - Carapa | 2014	-0.29	-0.41	-0.17	*	0.14	0.09	0.2	*
Anthonotha - Beilschmedia | 2014	0.27	0.18	0.36	*	0.1	0.04	0.16	*
Anthonotha - Santiria | 2014	-0.19	-0.28	-0.11	*	0.11	0.07	0.17	*
Beilschmedia - Carapa | 2014	-0.57	-0.65	-0.43	*	0.04	0.01	0.08	
Beilschmedia - Santiria | 2014	-0.47	-0.54	-0.37	*	0.01	-0.01	0.05	
Carapa - Santiria | 2014	0.09	0.05	0.16	*	-0.02	-0.04	-0.01	
Anthonotha - Carapa | 2015	-0.17	-0.24	-0.09	*	0.08	0.04	0.13	*
Anthonotha - Beilschmedia | 2015	0.19	0.11	0.26	*	0.12	0.08	0.18	*
Beilschmedia - Carapa | 2015	-0.35	-0.41	-0.26	*	-0.04	-0.07	-0.03	
2015-2014 | Carapa	-0.13	-0.22	-0.07	*	0.03	0.01	0.05	
2015 - 2014| Anthonotha	-0.01	-0.09	0.07		-0.03	-0.09	0.02	
2015- 2014 | Beilschmedia	0.08	0.01	0.16	*	-0.05	-0.1	-0.03	

With respect to nutrient content of the four, seed species, seeds with higher fat content consistently had a higher probability of being predated (Figure 5.7) and the differences between the fat content levels were significant (median DIC ≥ 10%) except for the difference between the 'high' and 'moderate' seed categories across all years (Table 5.4). Seed caching probabilities for the different fat content levels were the same (median DIC < 5%) except in the year 2014 where seeds with lower fat contents had a significantly higher probability of being predated (Table 5.4).

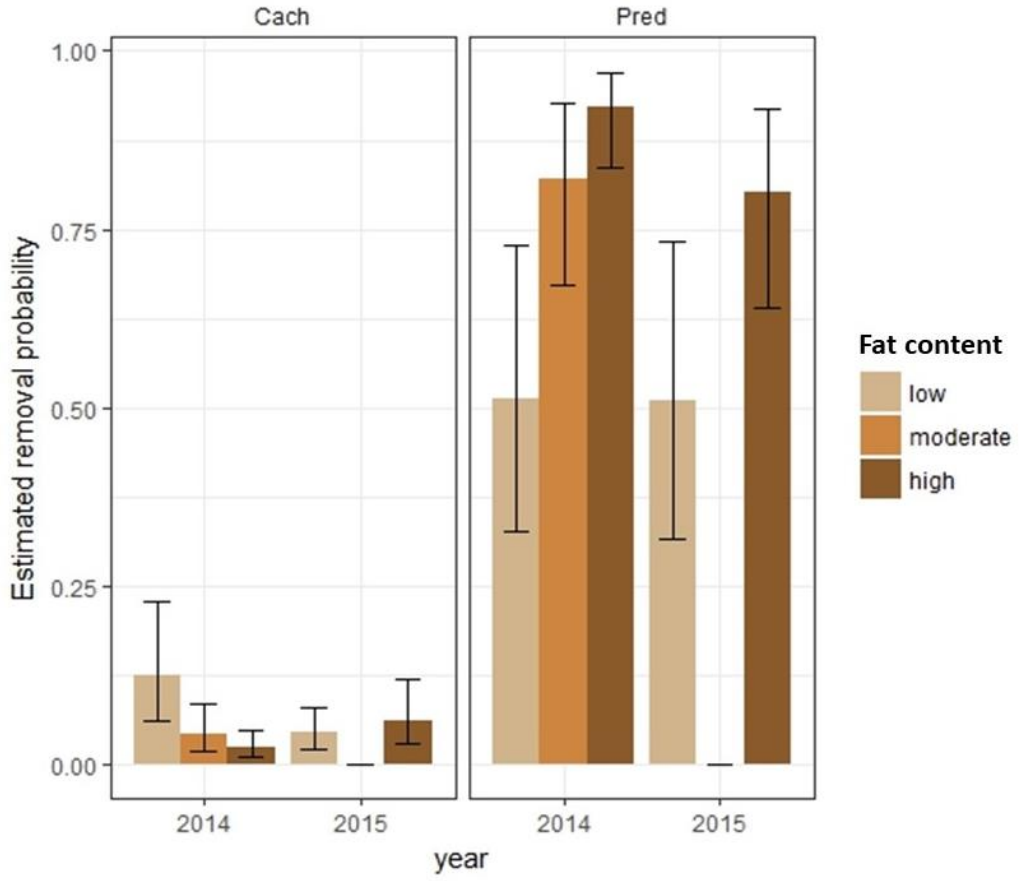

Figure 5.7: Estimated probability of seeds being predated or cached with respect to fat content levels (< 2% =low, > 2% <10 %= moderate,> 10% =high). Probability values were obtained by transforming ($1/(1+e^{(-\beta)})$) posterior distributions from a Bayesian binomial logistic regression. In all years except 2014, seeds with low fat content consistently had a significantly higher probability of being cached than all the seeds with moderate or high fat content. See Table 5. 4 for details on pairwise differences in probabilities.

Although seeds with 'moderate' protein content had a higher probability of being predated than seeds with 'low' protein content (median DIC > 8%) (Figure 5.8), there was no difference in the probability of seed caching based on this factor (median DIC < 5%) (Table 5.4).

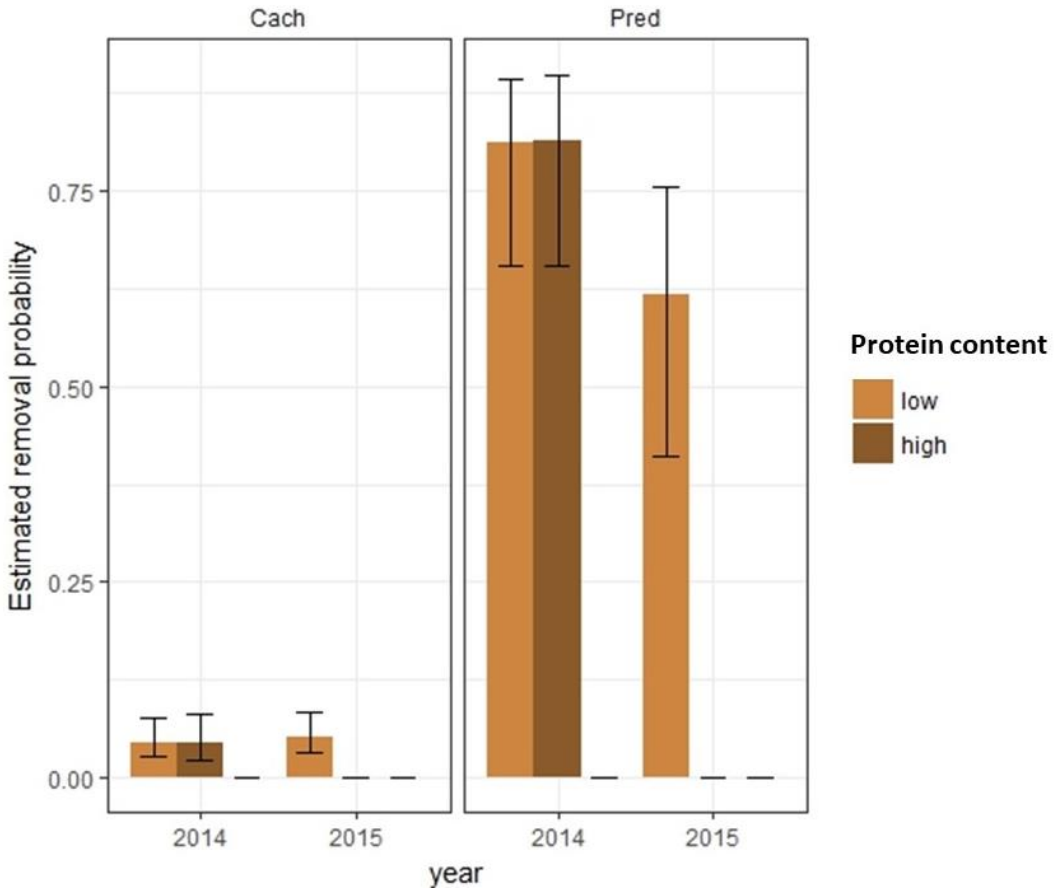

Figure 5.8: Estimated probability of seeds being predated or cached with respect to protein content levels (< 2% =low, > 2% <10 %= moderate,> 10% =high).

Probability values were obtained by transforming $(1/(1+e^{(-\beta)})$ posterior distributions from a Bayesian binomial logistic regression. There was no difference in seed caching probability with regards to protein content levels. (See Table 5. 4 for details on pairwise differences in probabilities).

Probability of seed predation was consistently and significantly higher for seeds with 'low' fibre contents (median DIC ≥ 10%) (Figure 5.9).

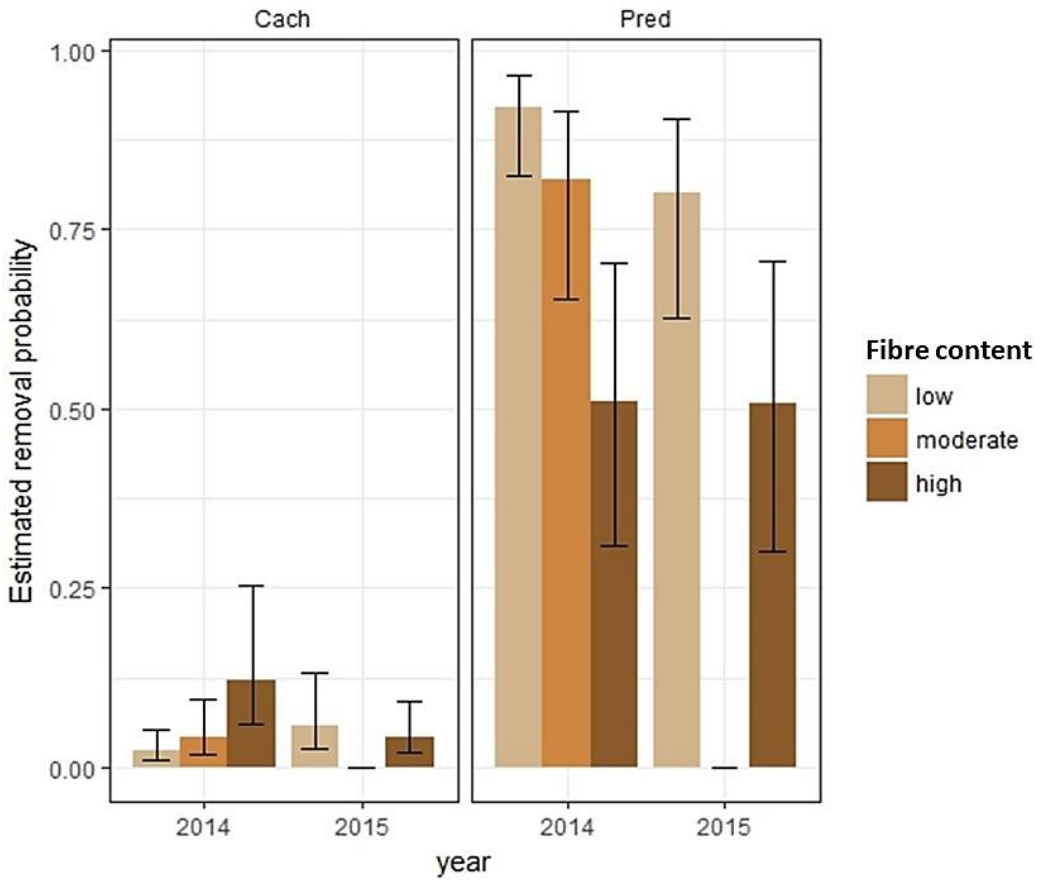

Figure 5.9: Estimated probability of seeds being predated or cached with respect to Fibre content levels (<10% =low, > 10% < 40%=moderate, >40%=high). Probability values were obtained by transforming ($1/(1+e^{(-\beta)})$) posterior distributions from a Bayesian binomial logistic regression. Seeds with lesser fibre contents were significantly predated than seeds with higher fibre content. Seeds with high fibre contents have a significantly higher probability of being cached in 2014. See Table 5. 5 for details on pairwise differences in probabilities.

There was no difference in the probability of seed caching based on fibre content except in 2014 where seeds with 'high' fibre content had higher probability of being cached (Table 5.5).

The probability of predation for a seed with 'high' carbohydrate content was higher than for seeds with 'moderate' carbohydrate content (Figure 5.10) and the pairwise difference was consistently significant (median DIC > 20%). The seed caching probability was the same for both the 'moderate' and the 'high' carbohydrate content categories except in 2014 where seed caching probability was significantly higher for 'moderate' than for 'high' carbohydrate content (Table 5.5). Additionally, the probabilities of caching for each carbohydrate level, did not differ between years (median DIC < 5 %).

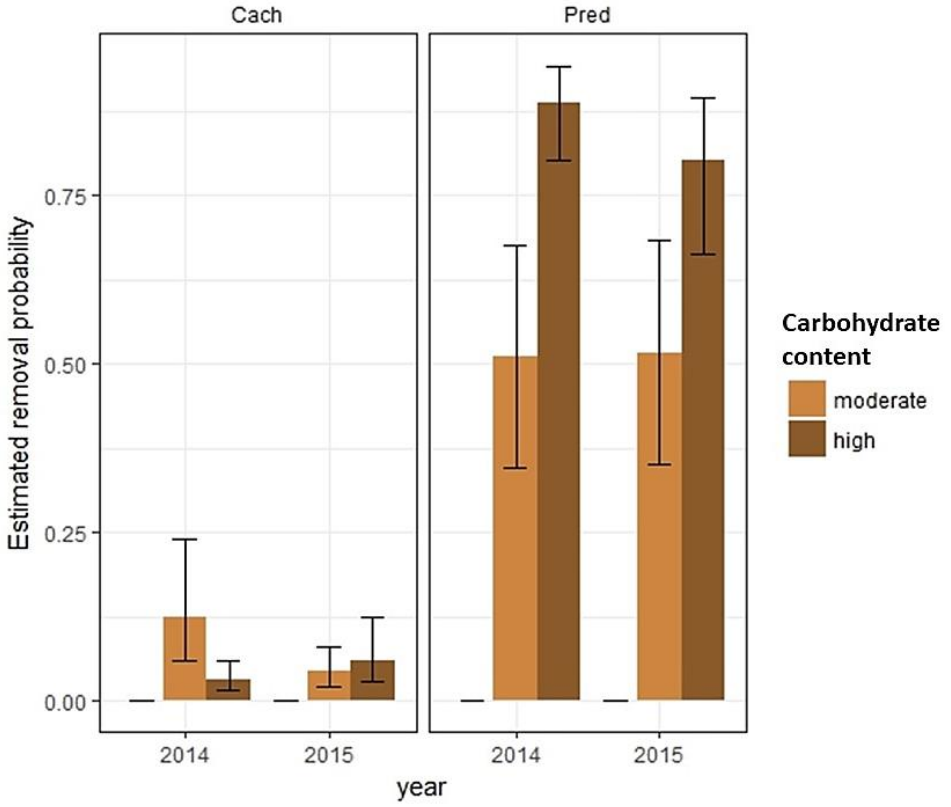

Figure 5.10: Estimated probability of seeds being predated or cached with respect to Carbohydrate content levels (<10% =low, > 10% <40 %=moderate, and > 40% = high). Probability values were obtained by transforming ($1/(1+e^{(-\beta)})$) posterior distributions from a Bayesian binomial logistic regression. For the average of all years and in all years, seeds with high carbohydrate content consistently had a significantly higher probability of being predated while those with moderate carbohydrate content had a significantly higher probability of being cached only 2014. See Table 5. 5 for details on pairwise differences in probabilities.

Of all the five external factors considered in the Bayesian models, fruit abundance consistently had a significant effect such that high fruiting periods were associated with slight increases in seed caching and decreases in seed predation. While understory herb density and percentage dead logs had significant effects on caching probabilities (All confidence limits < or > 0, see Appendix 5.3 to 5.12 for details).

Table 5.4: Pairwise posterior probability differences of seeds being predated and cached different based on levels of fat and protein contents in different years.

	Parameter differences	Predated				Cached			
Fat content		**Median**	**Lcl (2.5%)**	**Ucl (97.5%)**		**Median**	**Lcl (2.5%)**	**Ucl (97.5%)**	
	High - Moderate | All years average	0.01	-0.03	0.04		0.01	-0.01	0.03	
	Moderate - Low | All years average	0.31	0.20	0.37	*	-0.04	-0.07	-0.02	
	High - Low | All years average	0.31	0.20	0.37	*	-0.03	-0.06	-0.01	
	High - Moderate | 2014	0.10	0.04	0.16	*	-0.02	-0.04	-0.01	
	High - Low | 2014	0.41	0.25	0.51	*	-0.1	-0.17	-0.05	*
	Moderate - Low | 2014	0.30	0.20	0.37	*	-0.08	-0.14	-0.04	*
	High - Low | 2015	0.29	0.19	0.35	*	0.02	0.00	-0.04	
	2015-2014 | High	-0.12	-0.19	-0.05	*	0.04	0.02	0.07	
	2015-2014 | Low	-0.03	-0.05	0.05		-0.08	-0.14	-0.04	
Protein content									
	High - Low | All year average	0.09	0.05	0.13	*	-0.01	-0.02	0.01	
	High - Low | 2014	0.01	-0.03	0.03		-0.01	-0.02	0.02	
	2015-2014 | Low	-0.20	-0.25	-0.14	*	0.01	-0.01	0.02	

Table 5.5: Pairwise posterior probability differences of seeds being predated and cached based on different levels of fibre and carbohydrate contents in different years.

	Parameter differences	Predated				Cached			
Fibre		**Median**	**Lcl (2.5%)**	**Ucl (97.5%)**		**Median**	**Lcl (2.5%)**	**Ucl (97.5%)**	
	High - Moderate | All years average	-0.31	-0.37	-0.22	*	0.04	0.02	0.07	
	Moderate - Low | All years average	-0.16	-0.18	-0.14	*	-0.01	-0.03	0.01	
	High - Low | All years average	-0.31	-0.37	-0.21	*	-0.03	-0.01	0.06	
	High - Moderate | 2014	-0.31	-0.37	-0.22	*	0.08	0.04	0.15	*
	High - Low | 2014	-0.41	-0.51	-0.27	*	0.10	0.05	0.17	*
	Moderate - Low | 2014	-0.10	-0.17	-0.05	*	0.02	0.00	0.04	
	High - Low | 2015	-0.29	-0.36	-0.20	*	-0.02	-0.05	0.01	
	2015-2014 | High	-0.01	-0.05	0.05		-0.08	-0.15	-0.04	
	2015-2014 | Low	-0.12	-0.20	-0.06	*	-0.04	-0.02	0.07	
Carbohydrate									
	High - Moderate | All years average	0.29	0.22	0.34	*	-0.03	-0.06	-0.01	
	High - Moderate | 2014	0.37	0.28	0.45	*	-0.9	-0.16	-0.05	*
	High - Moderate | 2015	0.28	0.21	0.34	*				
	2015-2014 | High	-0.09	-0.14	-0.05	*	0.02	0.00	0.05	
	2015-2014 | Low	0.01	-0.05	0.05		0.03	0.01	0.06	

Although the species used in the experiments differed markedly in seed size, the differences in their dispersal kernels were not significant (median DIC < 5%). *Anthonotha* being the largest was not cached across a farther distance than *Santiria* which was the smallest (5.11).

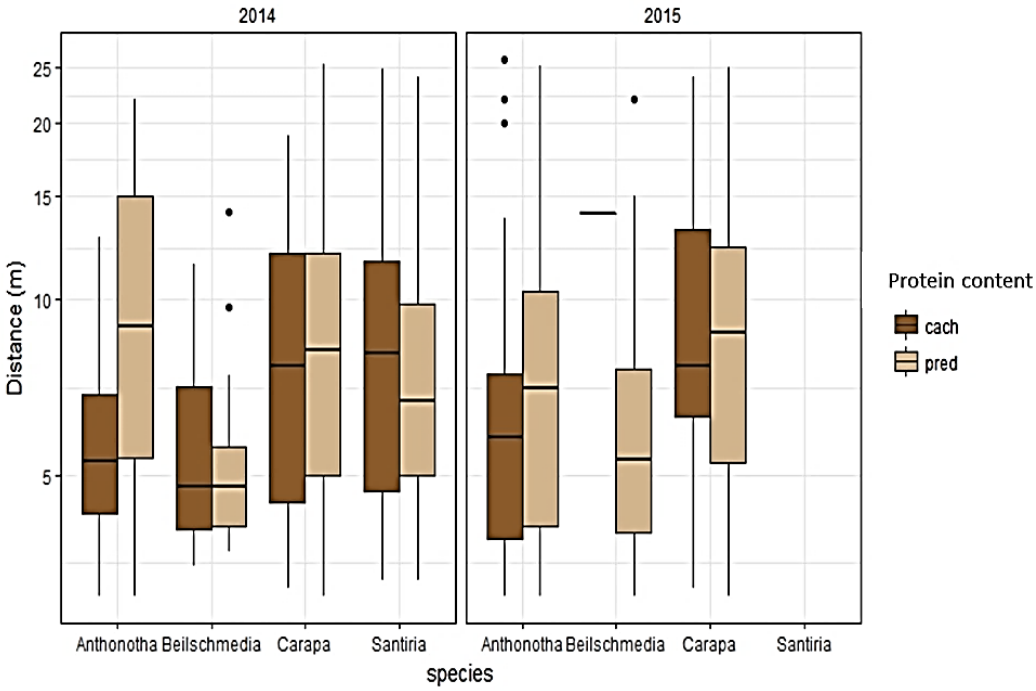

Figure 5.11: Observed distances of different seed species moved removed by large rodents in NNFR. The distances shown here are in $\log_{10}$ scale. (Box plots show median values (solid horizontal line), 50th percentile values (box outline) and 90th percentile values (whiskers) and outlier values (closed circles)).

The probability of survival for dispersed seed after a period of ten weeks in Kaplan-Meier survivorship curves, differed significantly by species (χ^2=73.3, df = 3; $p < 0.01$) but not by size (Figure 5.12). *Anthonotha* and *Beilschmedia* which had higher fibre contents survived longer than *Carapa* and *Santiria,* which were high in fat content (Table 5. 6).

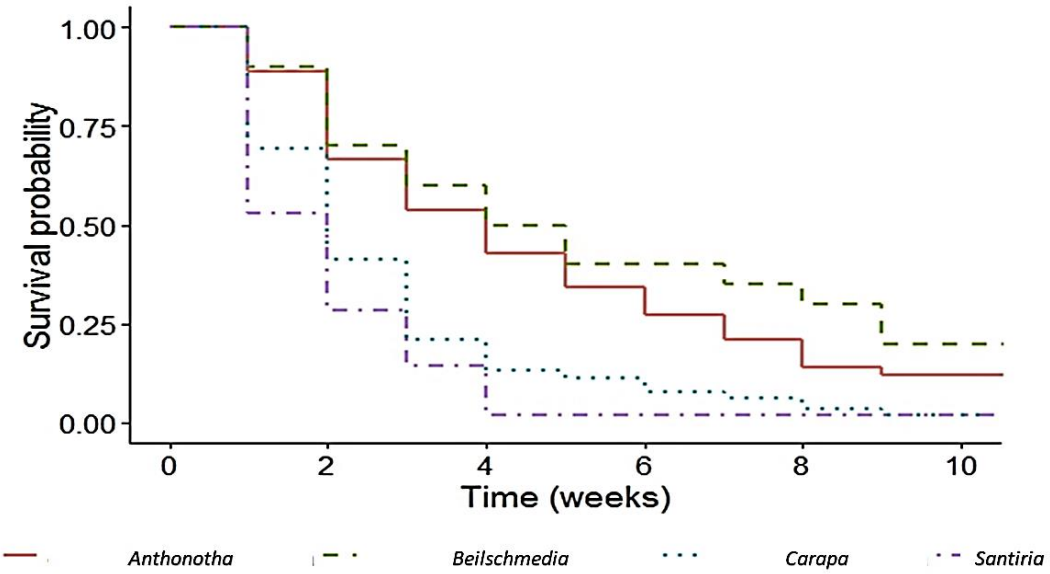

Figure 5.12: Survival probability ten weeks after being dispersed. Using a Kaplan-Meier survival test, *Beilshmedia* had a higher probability of survival compared with other species and the *Santiria* had the lowest probability of survival (seed Table 5.6)

Table 5.6: Number of seed species at risk after ten weeks based on the Kaplan-Meier survival test

Species	**Total number dispersed**	**Number at risk after 10 weeks**
Anthonotha noldae	240	29 (12.08%)
Beilschmedia manni	21	4 (19.01%)
Carapa oreophila	114	2 (1.75%)
Santiria trimera	49	1 (2.04%)

Figure 5.13: One of the few scatterhoarded *Anthonotha* seeds germinated and grew. The photograph was taken six months from the time it was cached.

5.3.1.1 Visiting rodents

Out of a total of 1,033 images captured by my motion-triggered camera traps during the first experiment, *Cricetomys* were the predominant visitors and accounted for 70% of the images. Only 17% of the images were of *Atherurus* while the remaining 13% consisted of other animals including birds which were not likely to interact with the seeds

(Figure 5.14).

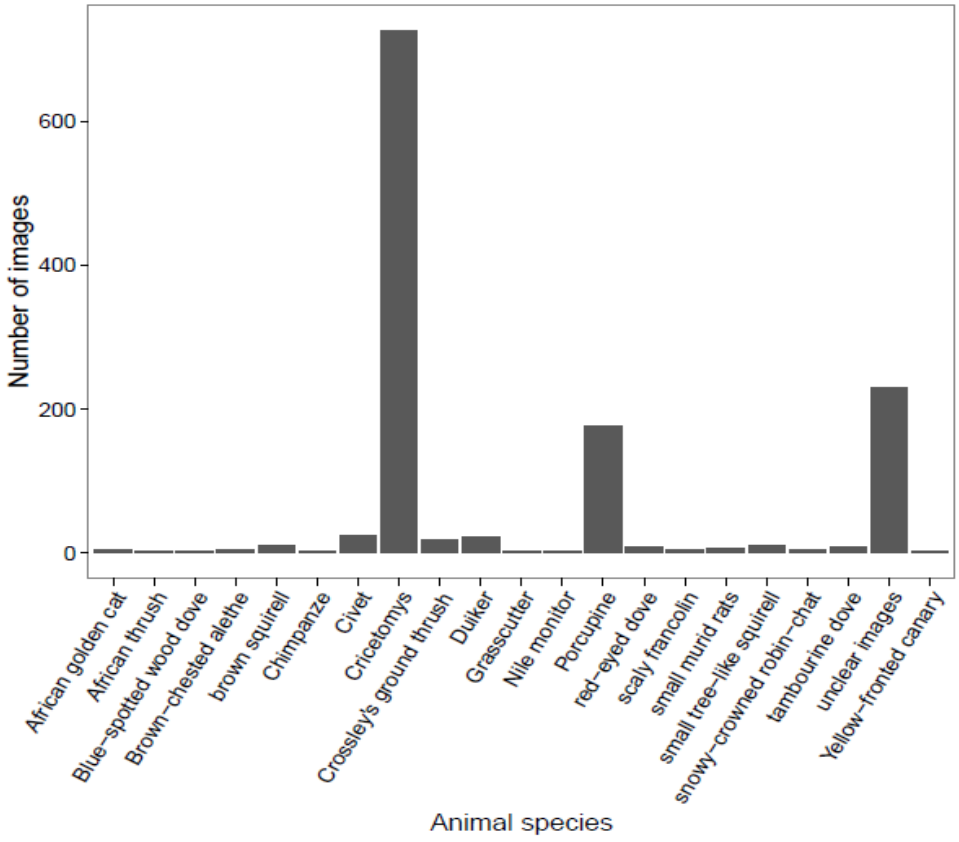

Figure 5.14: Animal species that visited experimental plots as captured by the camera traps placed during seed removal experiments.

5.3.2 **Intraspecific seed removal**

Of the 1620 *Carapa* seeds used in this study, 98 % (1,587) were removed and of these, 84% (1,333) were predated, 6 % (95) were cached and 10 % (159) were missing. There was a significant difference in seed fate between years (χ^2=53.56, df = 3; $p < 0.01$). There was no marked difference between the probability density function curves of the seed mass distributions for dispersed and predated *Carapa* (OVL=0.84). Similarly, the overlapping coefficient for the seed length distributions of dispersed and predated *Carapa* showed an apparent close fit (OVL=0.68) (Figure 5.15).

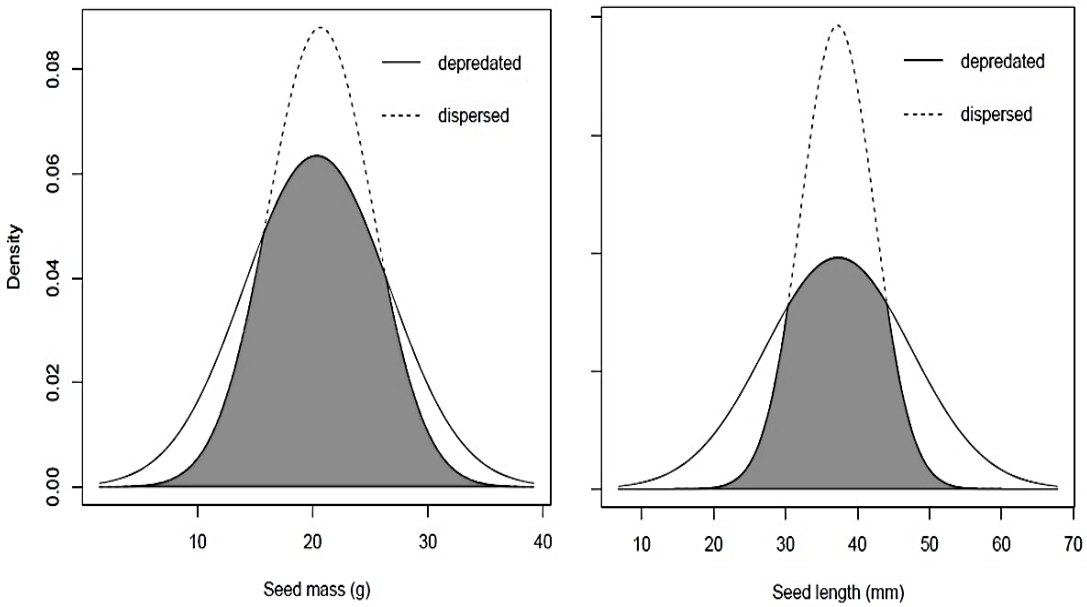

Figure 5.15: Probability density curve showing marked overlap of removed *Carapa* seeds in varying sizes that were predated and dispersed by scatterhoarding rodents.

The distances to which seeds were moved did not differ between the two years (t=1.77, df = 514.63, p = 0.08). Results from my best GAMM model showed no significant effect of seed size and seed length on dispersal distance of *Carapa* seeds (Table 5.7).

Table 5.7: Summary of results from a generalised additive mixed model to determine effect of seed size on dispersal distance. R-square (adj) = 0.017

Fixed effects	**Estimates**	**Standard error**	**t value**	**p value**
Intercept	313.45	112.12	2.80	<0.01
Year	-0.15	0.06	-2.27	0.18
S (seed mass)	-0.08	0.10	-0.833	0.12
S (seed length)	0.06	0.04	1.46	0.08

Cricetomys and *Atherurus* accounted for 92 % of the visitors based on images captured by my camera traps in this experiment. There were 337 and 167 images of *Cricetomys* and *Atherurus* respectively. Other animals captured included duikers, doves and squirrels, but based on the images, these animals did not interact with the *Carapa oreophila* seeds.

5.3.3 **Artificial seed removal**

All the artificial seeds placed in the 12 experimental sites were removed in less than six days. The rate of artificial seed removal was significantly greater in the wet season (mean = 19.14 seeds per day) than the dry season (mean = 16.29 seeds per day) ($U = 39$, $p = 0.03$) (Figure 5. 16). There was however, no difference in seed fate between the two seasons ($\chi^2 = 6$, $df = 4$, $p = 0.19$) (Figure 5.17). Additionally, for the months in which experiments were carried out, there was no relationship between the monthly seed removal rate and the monthly fruit abundance indices of large seeded species (Spearman's $R = -0.10$, $p=0.78$) or between the monthly seed removal rate and the overall monthly fruit abundance indices (Spearman's $R = -0.67$, $p = 0.23$). Furthermore, results from the Bayesian multinomial logistic model showed that there is an increase in the probability of caching seeds when fruit availability is high (Table 5.8).

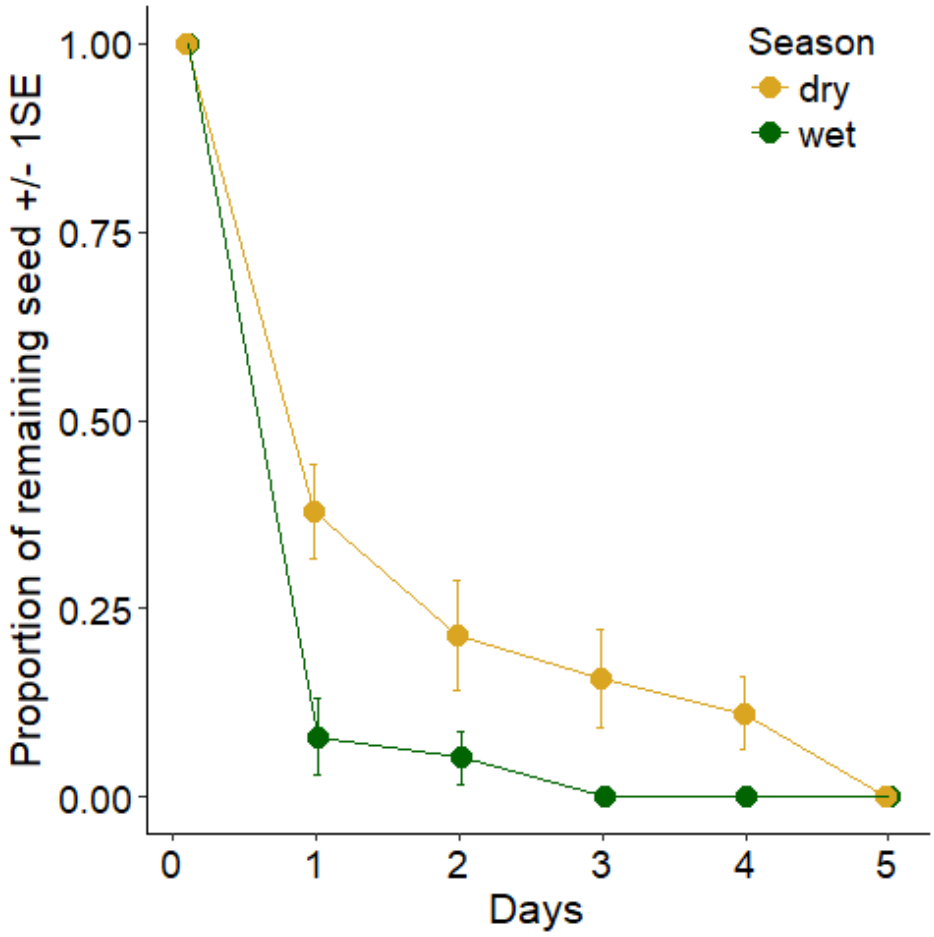

Figure 5.16: Average proportion of seeds remaining at sites were seeds were placed in the wet and dry seasons. Seed removal was faster in the rainy season

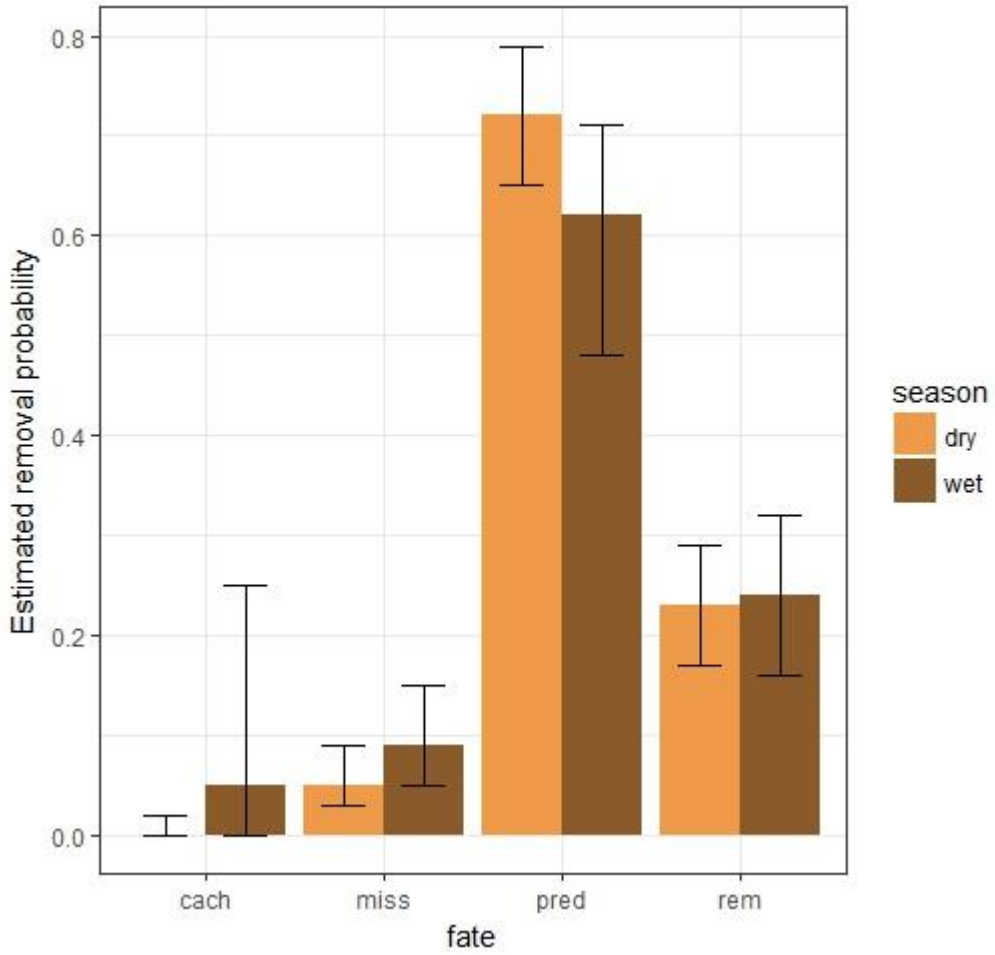

Figure 5.17: Fate of artificial seeds in the wet and dry seasons in NNFR. Probability values were obtained by transforming $(1/(1+e^{(-\beta)})$ posterior distributions from a Bayesian binomial logistic regression.

Table 5.8: Posterior probabilities of seed from a Bayesian multinomial logistic regression.

Parameters	**Cached**	**Missing**	**Predated**	**Remained**
Wet	0	0.05	0.72	0.23
Dry	0.05	0.09	0.62	0.24
Food abundance index	0.06	0.23	0.44	0.27

There was no significant difference between distance of removed seeds in the wet (mean = 7.37 m) and dry (mean = 7.34 m) seasons (t = 0.04, df = 217.69, p = 0.96) (Figure 5.17). Additionally, using a linear mixed effect model, season had no effect on the distances of removed seed but fruit availability had a marginal effect on the distances of removed seeds (Table 5.9)

Table 5.9: Effect of season and fruit availability on removal distance of artificial seeds in NNFR

Parameter	Estimate	Standard error	df	t-value	p-value
Intercept	2.56227	0.37715	369.5	6.794	<0.001**
Wet season	-0.06265	0.19877	414.6	-0.315	0.7528*
Fruit availability index	-0.08754	0.04503	405.7	-1.944	0.0526

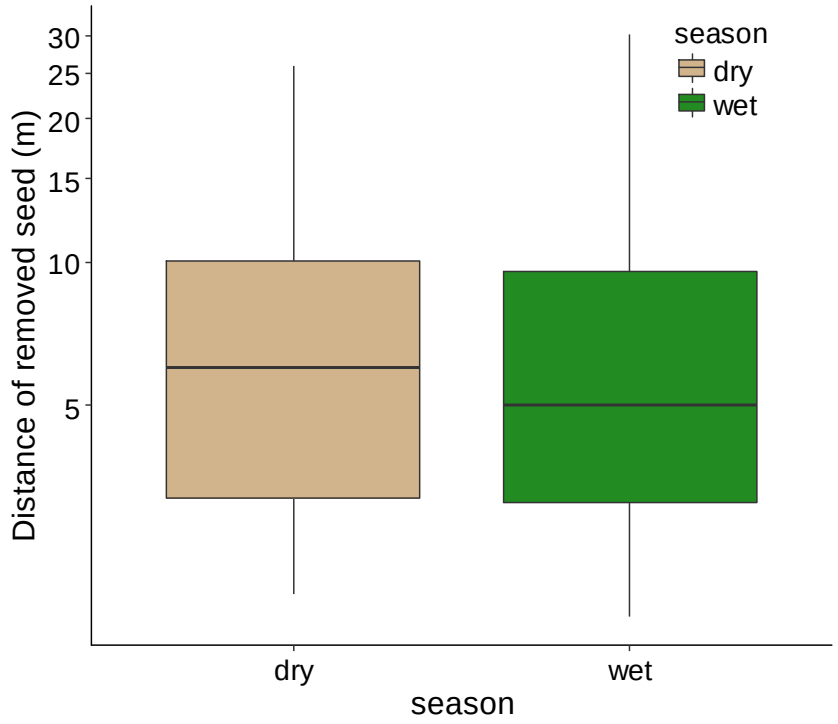

Figure 5.18: Box plots showing log scaled distances of removed seeds in the two main seasons in NNFR. The 25th, 50th and 75th percentiles are shown by the lower halves, middle lines and the upper halves of the boxes above while the whiskers represent the 5th and 95th percentiles of the data.

5.4 Discussion

The results from this study suggest that, in Afrotropical montane forests, predation and dispersal of large seeded species by large scatterhoarding rodents are most likely influenced by seed nutrient content and extrinsic factors such as fruiting season, rather than seed size. For example, *Santiria*, with the lowest mean seed mass had a higher rate of removal than *Anthonotha,* with the highest seed mass. This is in contrast to the findings of studies elsewhere which show that seed size is important (Jansen et al., 2004; Wang & Chen 2009; Yi & Wang, 2015). While my results do suggest that some large seeded species have higher probabilities of being predated than others, cafeteria experiments are still needed to confirm these results.

While *Cricetomys* was clearly a major seed remover, my camera trap images suggest that *Atherurus* also removes seeds. While this means that we have little evidence from field experiments that it is the rats that are scatterhoarding, a recent enclosure experiment I undertook at NNFR with only *Cricetomys,* showed for certain that the rats scatterhoard.

5.4.1 Seed predation and dispersal

The high rates of seed removal observed in this study (>80%) were similar to those recorded from other tropical studies (e.g. Forget, 1996; Nyiramana et al., 2011; Aliyu et al., 2014). Moreover, the high seed predation rates I recorded for all the seed species used in my study (up to 98% in *Carapa oreophila*) were also equivalent to predation rates recorded in other Afromontane studies. For example, the predation rate of *C. oreophila* seeds in this study was similar to that obtained by Nyiramana et al., (2011) for *C. grandiflora* seeds by African giant pouched rats in a Rwandan tropical montane forest. However, it now appears that Nyiramana et al. (2011) may have overlooked the possible contributions of *Atherurus*, which were sometimes observed in their study site (Pierre-Michel Forget, pers. comm.). However, in contrast to the similarity between my study and those from other

African sites, the rates of seed predation recorded by Aliyu et al. (2018) in his 2011 study were noticeably lower than in my study. The most likely explanation for this is that 2011 was an exceptionally high yielding year for *C*. *oreophila*.

Despite the high visitation rates of *Cricetomys* to my experimental plots, it is still not clear exactly what proportion of removed seeds were cached by *Cricetomys* relative to *Atherurus.* In agreement with the findings of Nyiramana et al. (2011), my results also suggest that at NNFR *Cricetomys* and/or *Atherurus* disperse only a small fraction of seeds on the forest floor. While the end result is very similar, African scatterhoarding behaviour differs to Neotropical rodents in that the latter typically remove seeds from the forest floor to a cache before predating them (Vander Wall et al., 2005b). In contrast, in Africa, almost all seeds are immediately predated on being discovered (Nyiramana et al., 2011). The final outcome is probably not so different, as only a small fraction of seeds were ever able to avoid predation and become established seedlings in both the Neotropics (Jansen et al., 2012) and Africa (Nyiramana et al., 2011; Seltzer et al., 2015). However, the survival and establishment of even a small proportion of seeds could have significant implications for plant recruitment and overall forest dynamics (Haugaasen et al., 2010).

5.4.2 Effect of seed nutrient content.

Although seed predators and dispersers are often attracted to seeds with high fat and protein content (Vander Wall, 2001; Wang & Chen, 2012), my study showed that protein was unimportant but species with higher quantities of fats were preferentially predated.

The extremely high probability of predation of *C. oreophila* relative to the other seed species I investigated is most likely because it has combination of large size and high fat content, both traits that have been shown to attract seed dispersers (Wang & Chen 2009, Wang et al., 2014). However, these same traits should theoretically, have made *C.oreophila* more prone to being dispersed than predated

(Wang & Chen 2009). It is possible that high predation of seeds with high fat contents is because seed predators use fat to compensate for the negative effects of dietary tannins in other seeds (Chung-MacCoubrey et al., 1997), however, relatively little is known about tannins in Afrotropical plants to support this assumption. This may explain why the very large seeded *Anthonotha* was found to be cached at the highest frequency of all seeds in my experiment; compared to other species it has lower levels of fats.

5.4.3 Survival of dispersed seed.

Results from the ten-week monitoring of dispersed seeds also corroborates the observations of Holl & Lulow (1997) who found that seed caching rodents preferentially retrieved some dispersed seed species over others. However, because the different seeds used in this experiment were available in different seasons, it is possible that the frequent retrieval of some seed species was more a consequence of the season in which the seed species was available rather than the inherent seed traits of the species.

Although most Neotropical tropical scatterhoarding rodents recover cached seeds within a short period, most of the recovered seed are re-cached rather than consumed (Vander Wall & Jenkins, 2003; Jansen et al., 2012). In contrast, my study showed that in Afromontane habitats most recovered seeds are predated upon immediately rather than being dispersed further. It is however, not clear whether food scarcity is the major driver of this behaviour or not.

The process of germination may use-up food reserves in seeds (Bradbeer, 1988) and may also reduce the concentration of defensive chemicals in some species, thereby reducing the likelihood of frequent retrieval of some seed species by scatterhoarding rodents (Steele et al., 1993; Yi et al., 2015). This may explain the infrequent seed retrieval of *Anthonotha* and *Beilschmedia* by *Cricetomys* in the current study. To explore this further, seeds will need to be tested for defensive chemical properties. High regeneration capacity may be important in countering rodent seed predation (Cao et al., 2011). However, in my study, of the few seeds of

Carapa and *Santiria* that did germinate, all of them had been predated within three weeks.

5.4.4 Dispersal distance

Most Neotropical scatterhoarding rodents remove seeds and carry them over relatively short distances before they are consumed or cached (Forget et al., 2005). This concurs with my findings; most of the removed seeds we found were within my 25 m radius of searching. Nevertheless, my hierarchical experimental design allowed me to inadvertently discover some seeds that were taken over longer distances than my search radius; in fact some of the seeds I found were carried up to 50 m away from their initial points before consumption. It is possible that *Atherurus*, which have larger home ranges and have been observed moving seeds over long distances (up to 46 m) in Gabon (Rosin & Poulsen, 2016b) may have been responsible for moving seeds over such distances.

In the Neotropics (Jansen et al., 2004) and in China (Wang et al., 2014) secondary caching of seeds often increases dispersal distance. In contrast I found that secondary caching was an extremely rare event in NNFR; out of the 424 seeds cached, I only observed four secondary caching events as most of the primarily cached individual seeds were eaten.

In contrast to many seed removal studies involving scatter hoarding rodents (e.g. Jansen et al., 2002; Jansen et al*.,* 2004, Wang et al., 2014) my results show that neither *Cricetomys* nor *Atherurus* carry larger seed species greater distances than small seed species. The mean dispersal distance for all the seed species used in my study did not differ significantly, even though the seeds differed markedly (*Carapa*: ~50-fold range) in size.

5.4.5 Intraspecific seed removal

This study showed that in Afromontane forests, intraspecific seed size is not a factor in the selection of seeds for immediate caching or predation by rodents, neither does

seed size influence dispersal distance of seeds removed by rodents. That seed size did not influence rodent decision-making in contrast with most previous findings (e.g. Brewer, 2001; Jansen et al., 2002; Wang & Chen, 2009; Galetti et al., 2010, Wang & Ives, 2017). However, while Theimer (2003) in Australia, found that medium sized *Beilschmedia bancroftii* seeds are more likely to be cached than larger and smaller seeds, he observed that seed size had no effect on dispersal distance.

Further, even though African giant pouched rats have a similar body size to Neotropical red acouchies (*Myoprocta acouchy*) and that the mean *C. oreophila* seed size (~21 g) in this study was similar to that of *C. procera* used in a comparable study by Jansen et al. (2004), the two sites yielded different results. While there was no correlation between seed size and caching distance in NNFR, there was a strong correlation in the study carried out in French Guiana.

I suggest two scenarios which may have led to this outcome in an Afromontane forest: i) food is less available in tropical montane versus lowland forest (Chapman et al., 2016) so that rodents are less choosy. This could also explain the high predation rates recorded in this study compared with those reported from lowland Neotropical forests (e.g. Forget, 1996; Jansen et al., 2004). ii) *Cricetomys*, the most abundant visitors to seeds in NNFR are omnivorous (Ajayi, 1977), so that seed size selection may not be as important to them as to the frugivorous-granivorous Dasyproctid rodents of the Neotropics (Dubost, 1988).

To my knowledge, this is the first study to determine the effect of seed size on seed selection and dispersal distance using a single seed species in Africa. The non-preferential selection for seed size by Afrotropical montane rodents may have been useful in maintaining genetic diversity in some montane forests of Africa as is the case with most animal-dispersed tree species (Hamrick et al., 1992).

5.4.6 Seasonal effect

This study has shown that seasonal fruit abundance in the wet and dry season has little or no effect on seed caching or seed predation by Afrotropical scatterhoarding rodents. It also appears that season has no effect on the distances seeds are dispersed within Afromontane forests. Smythe (1970) proposed that large-seeded species in tropical forests fruit in a relatively similar period to increase their chances of being hoarded by rodents. This means that seed hoarding should increase with fruit availability. While seasonal fruit abundance has been shown to affect the proportion of seed hoarding and predation by scatterhoarding rodents in some parts of the Neotropics (Forget et al., 2002; Haugaasen et al., 2010), and in an earlier experiment of this study, I found no strong evidence to suggest that the rodents in NNFR increase their hoarding activities in seasons when fruit is abundant. In contrast to Haugaasen et al. (2010) this study shows that the rate of seed removal was higher in the wet, than the dry season despite the higher fruiting yield of large-seeded species in the wet season. However, these results may have differed slightly if the experiment had been conducted during the lowest (October and November) and peak (April and May) fruit production period of most species (see Appendix 5.2). I did not choose these periods for my experiment because one of my main objectives was to determine the effect of distinct seasonal aridity and so I chose months that were within the distinct seasons.

Using artificial seeds as I have done in this study needs to be approached with caution; it is important that the seeds are not disproportionately preferred by rodents, especially when the background food resource is low. Foraging behaviour of rodents may be obfuscated if a highly preferred food or seed species is used (Holl & Lulow, 1997). While I did not test to see if the rodents in my study preferred the artificial seeds over real seeds, it is possible that the chances of finding the seeds by the rodents was considerably higher because of the peanut smell in the artificial seeds and because fruit availability is generally low in tropical montane forests (Chapman et al., 2016). Disproportionate removal of favourite seed species over others has been demonstrated in a cafeteria experiment by Holl and Lulow (1997).

These authors found that seeds of *Prunus* spp were quickly removed and predated while other seed species remained at different proportions.

Many studies have shown that seeds that are moved farther away from maternal trees and into safer sites have higher chances of survival (e.g. Jansen et al., 2012; Hirsch et al., 2012), especially during periods that will favour their germination and establishment. Germination during the wet season is rapid for many large seeded species in NNFR (pers. obs.) and this, in addition to Smythe's (1970) satiation hypothesis, could be a possible explanation for why most of the large seeded species fruit at the beginning of the rainy season. However, in contrast to my expectations, (I had expected that there would be more frequent caching events at farther distances during the wet season), fewer artificial seeds were cached during the wet than the dry season, and the distances of the removed and predated artificial seeds did not differ across seasons. I suggest that the low fruit availability, especially during the months of my study, may have caused the similarity in the removal rate of artificial seeds in both the dry and wet seasons.

5.4.7 Conclusion

In conclusion, this study has shown that seed dispersal in Afrotropical montane forests is more likely to be impacted by seed nutrient content and overall community level food abundance than seed size. This study also suggests that in seeds with sufficient fat rewards offered to rodents, seed depredation by *Cricetomys* and/or *Atherurus* is a more probable fate than is dispersal. However, a rodent's choice of seeds based on nutrient content may vary across fruiting seasons (Forget et al., 2002) and possibly years, so that cafeteria experiments need to be conducted during different fruiting seasons and years to clarify factors affecting seed choice by rodents and the fate of removed seeds. My study also suggests that hoarded seeds which offer low energy rewards for rodents, are less likely be retrieved. This study also showed that seed size was not a major factor influencing seed choice by Afromontane scatterhoarding rodents. Finally, my study has shown that seed predation is high in both rainy and dry seasons.

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Chapter 6: Synthesis

6.1 Background

Tree species diversity in Afrotropical forests is steadily declining due to a range of factors including forest fragmentation, hunting and grazing (Primack & Corlett, 2005, Barlow et al., 2016). Although forest fragmentation is considered the leading cause of species diversity loss (Lugo et al., 1993; Arroyo-Rodríguez et al., 2017), accumulating evidence suggests that dispersal limitation will most probably sustain the trend of biodiversity loss in tropical forests (Wunderle Jr, 1997; Vanthomme et al., 2010; Caughlin et al., 2015). Dispersal limitation is likely to be especially severe in Afromontane forests, which are mostly smaller in size compared with lowland forests (Chapman et al., 2016) and have fewer large mammalian seed dispersers. While commendable conservation efforts continue to be made by governments, national and international non-governmental organisations (NGOs) and conservation scientists to reduce anthropogenic degradation in tropical Africa (McNeely, 1993; Oates, 1999; Anthony et al., 2015), relatively little management efforts have been made to sustain or improve seed dispersal processes. For an effective application of management techniques in the long term conservation of Afrotropical forests, developing a good understanding of existing seed dispersal and plant recruitment processes, is essential. Because most tropical forest trees species (between 70 % and 94 %) rely on animals for seed dispersal (Wunderle Jr, 1997; Jordano et al., 2007), it is crucial to understand the contributions of each animal taxa in a forest.

Among the different animal groups involved in seed dispersal in Africa, large bodied frugivorous mammals have received the most research attention because of their roles in dispersing large-seeded species over long distances (Wrangham et al., 1994; Campos-Arceiz & Blake, 2011). Unfortunately, the populations of these large bodied mammals have reduced dramatically as a result of indiscriminate hunting and

habitat loss, resulting in increased levels of dispersal limitation among large seeded species (Vanthomme et al., 2010; Effiom et al., 2013;).

Nevertheless, numerous studies in the Neotropics have demonstrated the importance of small mammals in dispersing seeds (e.g. Forget et al., 1998, 2002, Jansen et al., 2004, 2012; Galetti et al., 2014) and more recently, emerging evidence suggests the case may be the same in Africa (Nyiramana et al., 2011; Aliyu et al., 2014). Small mammals have been found to be important role players in dispersal of large-seeded tree species through their scatterhoarding behaviour (Forget et al., 1998; Jansen et al., 2012; Aliyu et al., 2014). Scatterhoarding, a behaviour whereby animals collect food items/seeds from one location and store them singly in another location for future use, may inadvertently result in seed dispersal. This occurs when seeds of tree species are moved by such animals away from their parent plants to locations where they are abandoned/forgotten and subsequently grow and establish (Vander Wall, 1990). Jansen et al. (2012) showed how an extant cocosoid palm *Astrocaryum standleyanum* has depended on scatterhoarding rodents for its continuous existence following the extinction of its associated megafauna dispersers in the late Pleistocene era.

However, while the role of scatterhoarding rodents in seed dispersal has been relatively well established in the Neotropics (Forget et al., 1998, 2002; Brewer & Rejmánek, 1999; Jansen et al., 2004), relatively little is known on the role of scatterhoarding rodents in dispersing large seeded species in tropical Africa (Nyiramana et al., 2011; Aliyu et al., 2014; Rosin & Poulsen, 2017). Of the few studies involving African scatterhoarding rodents and seed dispersal, the African giant pouched rat (*Cricetomys spp*) has been identified as a potentially important seed disperser of large-seeded tree species (Nyiramana et al., 2011; Aliyu et al., 2014; Seltzer et al., 2015). Consequently, the main aim of this thesis was to study aspects of the behaviour of *Cricetomys sp.* nov in relation to its seed dispersal potential in Ngel Nyaki Forest Reserve (NNFR). Specifically, I investigated the distribution of *Cricetomys* sp. nov. in NNFR, its density in relation to tree species

distribution, its perception of predation risk and its foraging behaviour in relation to innate seed characteristics and season. Given the paucity of studies involving large rodents in Africa, this study is possibly the first to include other aspects of *Cricetomys* behaviour in seeking to establish its effectiveness as a seed disperser in an Afromontane forest. I investigated the density and distribution of *C. sp.* nov. in Chapters 2 and 3, while Chapter 4, I provided information on its perception of predation risk. In Chapter 5, I investigated the foraging behaviour of *C. sp.* nov. in relation to seed traits and season. Since little is known about *Cricetomys* ecology, my research started out with investigations into the distribution of the rat in NNFR; using live-trapping and camera trapping methods, I estimated their density across a range of habitats within NNFR.

6.2 Distribution and density of the African giant pouched rat in Ngel Nyaki Forest reserve

In Chapter 2 of this thesis, I have been able to show that *C. sp.* nov. was more abundant in the forest core compared with the forest edges and small forest fragments in NNFR and is almost never present in the grassland habitats. This finding agrees with Olayemi et al. (2012; Violaine Nicolas pers.comm) that *C. sp.* nov. is more closely related to *C. emini,* which commonly occurs in high forests than *C. gambianus* which prefers open, savannah habitats (Ray & Duplantier, 2013).

While I showed that *C. sp.* nov. individuals were overall, more abundant in the forest core, I found that their density distribution within the forest core was uneven. Rats were observed to be more abundant in some forest patches than others throughout the experimental year. The key factors responsible for the difference in population density across the forest patches in this study are yet to be determined. The low and high densities of *C. sp.* nov. observed in the early rainy and dry seasons respectively, suggest a possible population cycle among *C. sp.* nov. as is observed in many small mammals around the world (Batzli, 1992; Krebs, 1996). However, since *C. sp.*nov. are large and comparable to Neotropical acouchies in size (~1kg), their overal populatations are more likely to be stable all year round but

their densities may concentrate at different forest sites within the year (Pierre-Michel Forget pers. comm). I have also found that there is an apparent difference in the density of male and female *C. sp.* nov. in NNFR; the number of males trapped were constantly higher than females. I have explained this finding in terms of possible behavioural differences between the sexes and possible differences in sex-ratios at birth.

6.3 Home range

In terms of movement and home ranges of *Cricetomys* in montane forests, my study (Chapter 2) has provided the first estimates of movement ranges and home range size in their native habitat. Although *C. sp.* nov is comparable to the Neotropical acouchy in size, the estimated home range size of *C. sp.* nov. in this study (HR_{95} = 4.03 ha; HR_{50} = 0.31 ha) was smaller than the minimum home range size of the acouchy (HR_{95} = 6.50 ha). My finding is however, similar to Engeman et al. (2006) which reported that *Cricetomys* home ranges in their native habitats are small. However, the home range size from my study was also found to be smaller than the reported home range size estimated for *C. gambianus* i.e. ~ 5 ha (see Ray & Duplantier, 2013). This probably means that seed dispersal by *C. sp.* nov in NNFR may occur over short distances because the rats are more active within their home ranges.

6.4 Density

My estimates of rat density (Chapter 2) varied, depending on the methods used. Live-trapping and Spatially Explicit Capture Recapture (SECR) methods used within the forest core, gave an estimated density of 6.29 rats/ha. This was considerably higher than estimates from camera traps and a Random Encounter Model (REM) (3.31 rats/ha). There are two possible explanations for this discrepancy; i) the number of camera traps (eight) were far fewer than the number of live traps (64) used and ii) the camera trap locations may have been far away from the rats' home range centres. Considering the small size of the *C. sp.* nov. home range core, surveying its density with camera traps may either require many camera traps or a

few camera traps in multiple locations. Nevertheless, this study has shown that camera traps and REMs can be used to determine the abundance of *C. sp.* nov. and possibly other smaller mammals with the same behaviour in different habitats.

6.5 Relationship between the distribution of *Cricetomys* and large-seeded tree species in NNFR

In Chapter 3 of this study, I also showed that the abundance of *C. sp.* nov. burrows, was positively related to the abundance of large-seeded species. This finding is related to that of Aliaga-Rossel et al. (2008) who showed that scatterhoarding rodents are more abundant in areas with relatively higher densities of large-seeded trees. In their study, Aliaga-Rossel et al. (2008) found the Central American Agouti (*Dasyprocta punctata*) to be more abundant where more of its safe refuges were present. Considering the small home ranges of *C. sp.* nov. it is reasonable that they would occupy areas with more abundant food resources. Since burrows provide both nesting and safety, *C. sp.* nov. may disproportionately have more burrows in sites where food is abundant as the risk of predation may equally be higher in food-rich areas. However, the possibility of individual rats having multiple burrow exits, which could be a confounding factor is yet to be determined for *C. sp.* nov. Out of 45 burrow excavations, Ajayi (1977) found that any one individual *C. gambianus* burrow had a maximum of four burrow exits, and the longest distance between any two exits was 3 m. If the pattern of burrowing by *C. sp.* nov. is similar to that of *C. gambianus,* then it suggests that the density of rats can be inferred from the density of burrows in my study because the small plots searched for burrows, were at least 5 m apart.

6.6 Does *Cricetomys* predation risk vary in different microhabitats?

Contrary to most studies, which show that the perception of predation risk by small mammals is higher in open areas compared to areas with 'bushy' vegetation cover (see Verdolin, 2006), I found that *C. sp.* nov. does not perceive microhabitats with dense understory vegetation as safer sites compared to the open microhabitats

within the forest core (Chapter 4). One important explanation of this finding is the possibility of the rat's relative invulnerability to predators owing to its relatively large size (~1 kg) as observed in Neotropical acouchies, which are similar in size (Pierre-Michel Forget pers. comm). It is also possible that large predators, which could pose a serious threat to *C. sp.* nov., do not occur in sufficient numbers to elicit a discernible expression of the rat's perception of predation risk. Another possible explanation to the insignificant effect of microhabitat differences on *C. sp.* nov.'s perception of predation risk is behavioural modulation of predation risk (Brown & Kotler, 2004). Although behavioural modulation of predation risk can be achieved through intense vigilance or apprehension of predators, it is still unclear whether or not *C*. sp nov. detects its predators via sight or smell. Ibe et al., (2014) found that high olfaction acuity of *C. gambianus* correlates with the functional morphology of its brain; a trait which may be widespread in the genus *Cricetomys*. Thus, *C. sp.* nov. could potentially be more effective at modulating its predation risk via olfaction. The fact that *Cricetomys* can utilize all the microhabitats within its home range suggests that it can potentially depredate or disperse seeds in all microhabitats.

Interestingly, I also found that *C. sp.* nov. individuals seem to quickly learn about and memorize the location of food sources within their home range; this is evidenced by the continuous decrease in the mass of remaining corn seeds (*Zea mays*) following each consecutive day of replenishing these on the feeding trays in my 'Giving Up Density' GUD experimental sessions. This finding suggests that *C. sp.* nov. seem to retain a memory of the location of food sources within its home range. Having a relatively detailed understanding of where food can be found within its home range can be especially advantageous for these rats particularly in tropical montane forests where fruit yield of large-seeded species is lower compared to lowland forests (Chapman et al., 2016). The amount of seed remaining on the feeding trays was significantly affected by the total amount of seed initially placed on the feeding tray; this is surprising because these rats are known to collect seeds in their cheek pouches and hoard them at different locations. It is possible that the

corn seeds did not possess the traits that favour seed removal by these rats i.e. size and nutrient content.

Although there was no significant effect of microhabitats on the perception of predation risk of *C. sp.* nov. in this study, I observed that the perception of predation risk was higher at sites that were closer to the forest edge than those that were in the core of the forest. It could be then, that predators are more abundant in the forest edge than in the forest core. The risks at forest edges may be higher because both forest and grassland predators intersect at the forest edge in the process of hunting.

6.7 How do innate seed properties, food abundance and season *Cricetomys* foraging behaviour?

By using four large seeded species i.e. *Anthonotha noldae*, *Beilschmedia mannii*, *Carapa oreophila* and *Santiria trimera* for seed removal experiments in this study, I was able to determine, that over 50% of the seeds were predated in all cases except for *Beilschmedia mannii*, which were mostly ignored by the rodents (Chapter 5). In all cases less than six per cent of the seeds were cached and most of the cached seeds were later consumed by this rodent. Since about 70 % of the animals that interacted with seeds in the experimental plots were *C. sp.* nov., the conclusion can be made, that they are predominantly predators, and that their role as seed dispersers is minimal. However, this high rate of seed predation may be a response to low fruiting years. Tree phenology data collected by the Nigerian Montane Forest Project (NMFP) over the last 12 years evidently explains why a similar experiment by Aliyu (2014) found a higher percentage of seed caching (≥ 20 %) for all the seed species used in the year 2011. It is also possible that inter-annual population cycles of scatterhoarding rodents may influence seed fate; a hypothesis that is yet to be investigated.

Among the seed species used in this study, I found no evidence to suggest that larger seed species have higher probabilities of being predated or hoarded by *C. sp.* nov (Chapter 5). Despite controlling for seed type by using only one seed species (*Carapa oreophila*) with widely varying seed sizes (up to 50 fold range in mass), *C. sp.* nov. showed no apparent selection of size for either predation or hoarding. I proposed two possible explanations for this finding. Firstly, the relatively low abundance of large seeds on the forest floors of montane forests (Chapman et al., 2016) cause these rats to immediately remove encountered seeds either for predation or dispersal without necessarily considering its size. Secondly, the fact that *C. sp.* nov. is omnivorous (Ajayi, 1977; Ray & Duplantier, 2013) suggests that selection for seeds based on size may not have been an evolutionarily enforced behaviour since they can easily augment their energy requirements by eating invertebrates. In contrast, herbivorous scatterhoarding rodents of the Neotropics e.g. agoutis and acouchies have a strong size-based selection for seeds (Jansen et al., 2004).

Dispersal distances of seeds species removed in this study also had no relationship with seed size. This finding contrasts with studies in the Neotropics, which mostly demonstrate a positive relationship between seed size and dispersal distance (Forget et al., 1998; Galetti et al., 2010; Jansen et al., 2004).

Although seed size was not important in seed selection by *C. sp.* nov. in this study, I found that seed nutrient content such as fat and fibre were significant in determining the fate of seeds removed by these rats. Seed with higher fat content had a higher probability of being predated whereas seeds with lower fat content had a slightly higher probability of being dispersed. On the other hand, seeds with lower fibre content has a higher probability of being predated and seeds with higher fibre content had a higher probability of being cached and dispersed. Apparently, highly nutritious large-seeded species are more prone to post-dispersal predation in NNFR during years of low fruiting years.

Among all the extrinsic factors considered in this study, only fruit abundance was found to influence seed removal by *C. sp.* nov. The probability of dispersal was apparently higher when fruit abundance was relatively high. Seasonal aridity was found to have no effect on seed predation/dispersal ratio.

6.8 Future work

Despite the new knowledge on *Cricetomys* sp. nov. behaviour and its potential for seed dispersal in NNFR provided by this study and a previous study by Aliyu (2014), much remains to be learned about *C. sp.* nov. and its relationship with large-seeded species in NNFR and within African forests in general. Relatively little is known about the co-occurrence of *C. sp.* nov. and *Atherus africanus* in NNFR and I recommended that future studies should seek to determine the relative contribution of *A. africanus* to seed dispersal and/or predation. A long-term study on seed removal and *C. sp.* nov. population changes should provide details on conditional seed dispersal/predation by *C. sp.* nov. in NNFR. Finally, using artificial seeds with different nutrient concentrations could lead to a more refined understanding of how seed chemical properties enhance seed removal and seed fate through the activity of these rodents.

6.9 Conclusion

In conclusion, this study has provided useful behavioural information which may have possible applications in the taxonomy of *Cricetomys* spp and conservation of large-seeded species in montane forests. The density estimates of *C. sp.* nov. provided by this study will serve as a baseline for future comparisons in NNFR or with other geographical areas. This study has shown that dispersal by *C. sp.* nov. most probably only occurs within the main forest and so, active planting of large seeded species in the forest fragments and the grasslands may provide an alternate means of increasing the abundance of large seeded species in other parts of the forest.

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Appendices

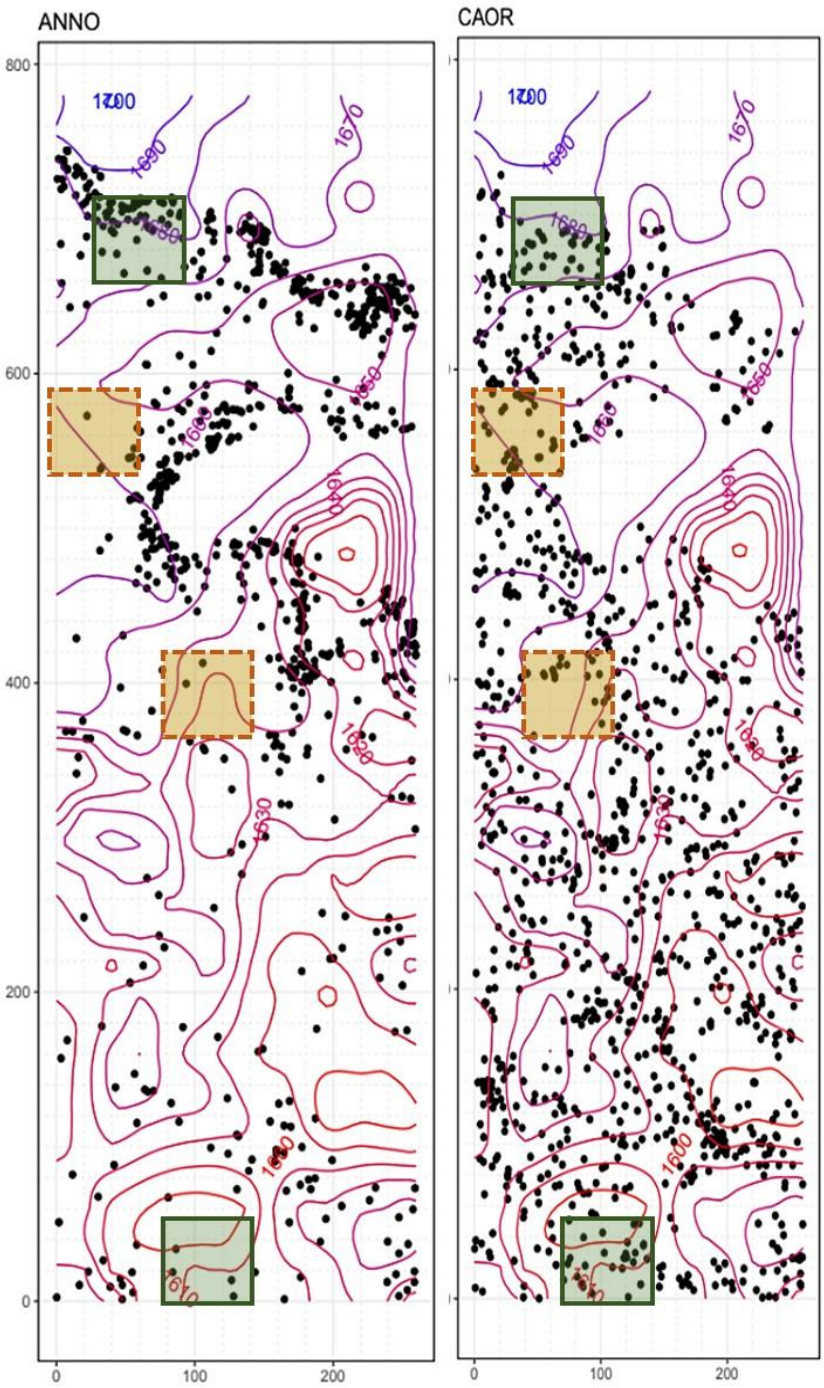
Appendix 2. 1: Change in Cricetomys morphometrics between long intervals of trapping. The seven individuals in the table below are the only retrapped individuals that still had one or both ears tags for > ½ year.

ID	Approx. Weeks	Δ Head length (cm)	Δ Body length (cm)	Δ Tail length (cm)	Δ Weight (kg)
4001	54	2.5	8.0	7.8	0.06
4101	53	0.0	2.1	3.0	-0.07
4151	37	0.5	3.1	0.0	-0.07
4155	37	0.5	2.0	2.5	0.24
4105	52	0.1	0.0	3.2	0.05
4031	53	0.0	0.0	1.2	-0.06
4011	52	0.4	6.5	3.2	0.22

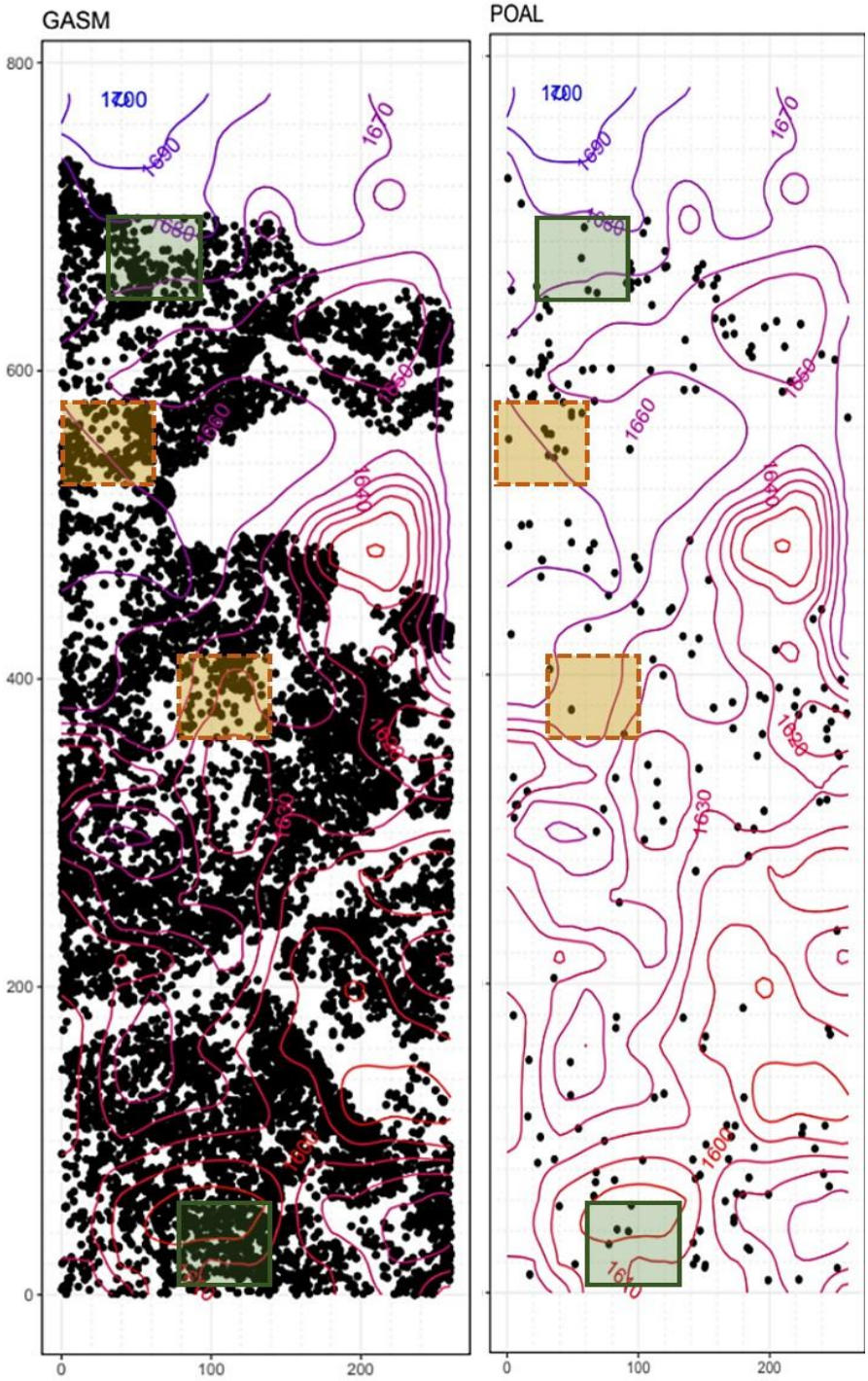
Appendix 2. 2: List of top 20 best models that fitted *Cricetomys* capture history; the models were selected out of 60 initial models based on least AIC values. The models below show the effect of site (k), sex (h), site transient response (K), response behaviour and site interaction (bk), number of burrows (burrows), percentage understory herb density (understory herbs) and average slope (slope) on either the capture probability (g0), or spatial scale (σ). For the models below density (D) was set to be constant i.e. 1.

Model	Npar	logLik	AIC	AICc	dAICc	AICcwt
g0~1, σ ~k	4	-1046.56	2101.12	2101.42	0	0.63
g0~h, σ ~k	5	-1046.01	2102.02	2102.48	1.06	0.37
g0~t, σ ~k + t	12	-1050.02	2124.04	2126.56	25.13	0
g0~K, σ ~K	5	-1083.85	2177.70	2178.16	76.74	0
g0~K, σ ~1	4	-1090.51	2189.01	2189.32	87.90	0
g0~1, σ ~K	4	-1098.45	2204.89	2205.20	103.76	0
g0~bk + burrows, σ ~h2	6	-1151.06	2314.11	2314.76	213.34	0
g0~bk + burrows, σ ~bk	6	-1151.76	2315.51	2316.16	214.73	0
g0~bk, σ ~1	4	-1154.93	2317.85	2318.16	216.73	0
g0~bk + slope, σ ~1	5	-1154.87	2319.74	2320.20	218.78	0
g0~bk + understory herbs, σ ~1	5	-1155.34	2340.81	2341.05	218.85	0
g0~K + no.holes, σ ~1	5	-1156.34	2389.40	2390.84	220.23	0
g0~K + understory herbs, σ ~1	5	-1156.51	2399.10	2399.61	221.02	0
g0~h + burrows, σ ~1	5	-1156.69	2419.04	2420.19	221.81	0
g0~h + burrows, σ ~1	5	-1154.88	2433.21	2434.09	226.03	0
g0~t + burrows, σ ~1	5	-1158.04	2467.37	2467.89	232.67	0
g0~t + burrows, σ ~k+t	7	-1159.79	2481.73	2482.05	232.90	0
g0~bk + burrows, σ ~k	6	-1161.03	2498.82	2499.19	238.85	0
g0~bk + burrows, σ ~t	6	-1163.02	2502.44	2502.99	242.74	0
g0~K + burrows, σ ~1	5	-1167.82	2522.91	2523.27	248.42	0

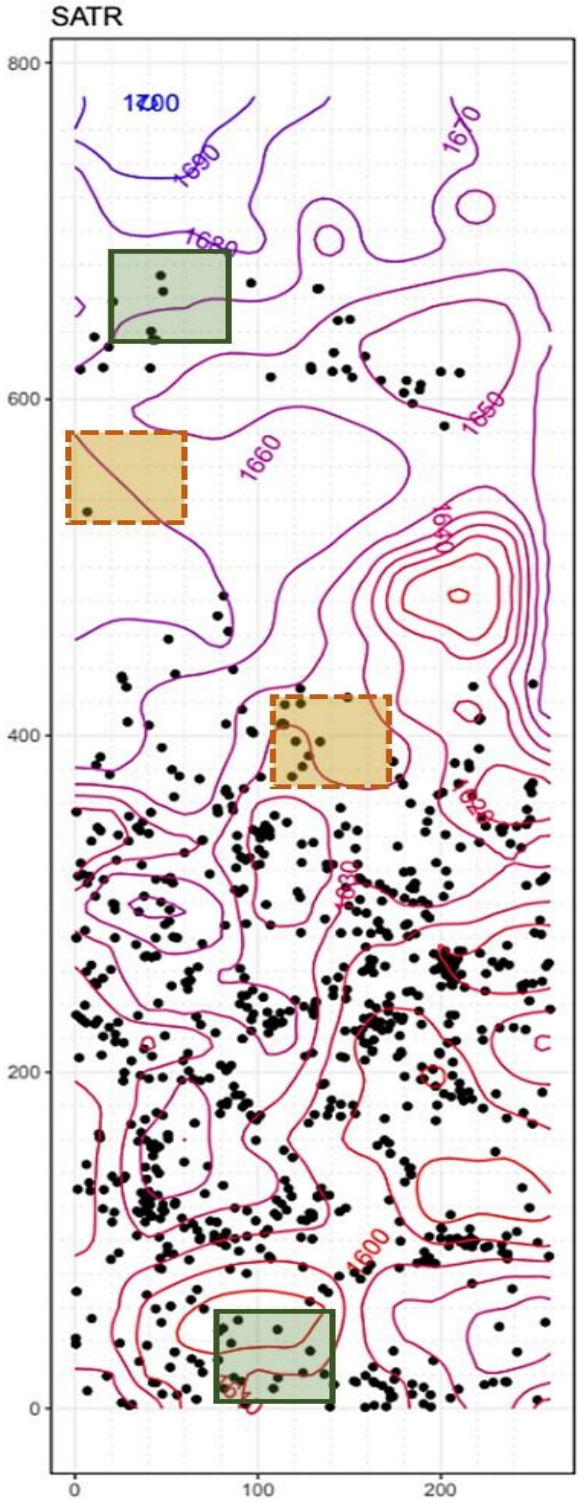
Appendix 3. 1: Spatial distribution of *Anthonotha noldeae* (ANNO) *and Carapa Oreophila* (CAOR) within the CTFS-ForestGEO plot in Ngel Nyaki Forets Reserve, Nigeria. Boxes with broken lines represent sites with low abundance of large-seeded species while boxes with solid lines represent sites with high abundance of large-seeded species. Black dots represent species locations.



Appendix 3. 2: Spatial distribution of *Garcinia Smeathmannii* (GASM) and *Pouteria altissima* (POAL) within the CTFS-ForestGEO plot in Ngel Nyaki Forets Reserve, Nigeria Boxes with broken lines represent sites with low abundance of large-seeded species while boxes with solid lines represent sites with high abundance of large-seeded species. Black dots represent species locations



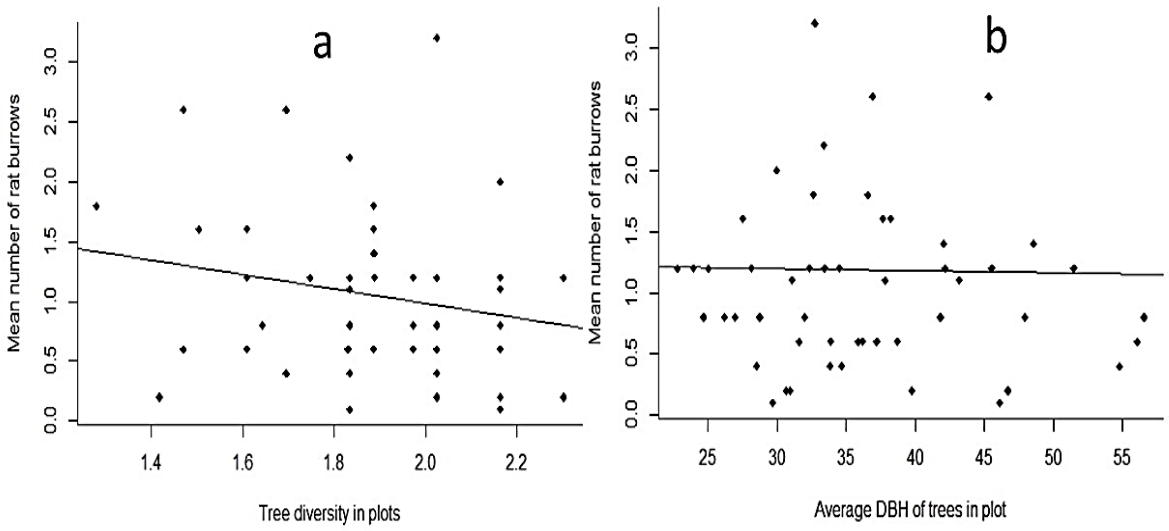
Appendix 3. 3: Spatial distribution of *Santiria trimera* (SATR) within the CTFS-ForestGEO plot in Ngel Nyaki Forest Reserve, Nigeria. Boxes with broken lines represent sites with low abundance of large-seeded species while boxes with solid lines represent sites with high abundance of large-seeded species. Black dots represent species locations



Appendix 3. 4: List of tree species recorded in small plots. Size category refers to seed size of the species.

s/n	Plant species	Size category		Plant species	Size category
1	*Albizia gummifera*	Small	24	*Lovoa trichiloides*	Small
2	*Anthonotha noldeae*	Large	25	*Macaranga monandra*	Small
3	*Beilschmiedia mannii*	Large	26	*Margaritaria discoidea*	Large
4	*Bombax* sp	Small	27	*Newtonia buchananii*	Small
5	*Campylospermum schefferi*	Small	28	*Nuxia congesta*	Small
6	*Carapa oreophila*	Large	29	*Oxyanthus speciosus*	Large
7	*Celtis gomphophylla*	Small	30	*Parkia filicoidea*	Large
8	*Chrysophyllum albidum*	Small	31	*Pavetta corymbosa*	Small
9	*Cordia millenii*	Large	32	*Pleiocarpa pycnantha*	Small
10	*Dasylepis racemosa*	Small	33	*Polyscias fulva*	Small
11	*Deinbollia pinnata*	Small	34	*Pouteria altissima*	Large
12	*Diospyros monbuttensis*	Large	35	*Ritchiea albersii*	Small
13	*Discoclaoxylon hexandrum*	Small	36	*Rothmania urcelliformis*	Large
14	*Dombeya ledermannii*	Small	37	*Santiria trimera*	Large
15	*Drypetes gossweileri*	Large	38	*Strombosia schefflera*	Small
16	*Entandrophragma angolense*	Large	39	*Symphonia globulifera*	Small
17	*Ficus* sp	Small	40	*Tabernamontana contorta*	Large
18	*Garcinia smeathmannii*	Large	41	*Trichilia welswitchii*	Small
19	*Harungana madagascariensis*	Small	42	*Trilepisium madagascariensis*	Large
20	*Isolona deightonii*	Large	43	*Voacanga bracteata*	Large
21	*Khaya grandifolia*	Large	44	*Warneckea* sp	Small
22	*Kigelia Africana*	Large	45	*Xymalos monospora*	Small
23	*Leptalus zenkeri*	Small	46	*Zanthoxylum leprieurii*	Small

Appendix 3. 5: No significant relatioship between density of rat burrows and tree diversity (a) or between density of rat burrows and tree size (dbh) (b).



Appendix 5. 1: Determination of proximate composition

1. Ash content determination

The term ash refers to the residue left after the combustion of the oven dried sample and is a measure of the total mineral content. Determination of ash content was carried out according to the method described in AOAC (1990).

Six crucibles were preheated in a muffle furnace at about 550^{o}C. Each crucible was cooled in a desiccator and weighed. Approximately 1g of each sample was weigh into the different crucibles. The crucibles and their contents were transferred into the muffle furnace at 550^{o}C and allowed to stay for 5 hours. The weights of the crucible contents were taken and recorded.

Percentage ash was calculated using the expression below

$$\% \, ash = \frac{Weight \, of \, ash}{Weight \, of \, dry \, sample} \times 100$$

2. Determination of moisture content

The method employed for the determination of moisture content of the samples was based on the measurement of the loss in weight due to drying at a temperature of about 105^{o}C as described in AOAC (1990).

Six watch glasses were washed and dried in an oven at about 105^{o}C after which they were cooled and weighed empty. Two grammes of each sample were weighed into their respective watch glasses. The watch glasses and their contents were dried in an air circulated oven at about 105^{o}C to a constant weight. The watch glasses and their contents were cooled in desiccators and reweighed.

The percentage moisture content of each sample were calculated using the expression

$$\%\ moisture\ = \frac{Loss\ of\ weight\ on\ drying(g)}{Initial\ sample\ weight} \times 100$$

3. Determination of crude lipid content

The lipid content of each sample was determined by the procedure described in AOAC (1990). A clean dry round bottom flask containing anti bumping granules was used. Exactly 210 cm^3 of petroleum ether (60 – 80^oC) into a flask fitted with soxhlet extraction unit. The weighed sample was transferred into a thimble already fixed into the Soxhlet extraction unit. Cold water was put into circulation. The heating mantle was switched on and the heating rate adjusted until the solvent is refluxed at a steady rate. Extraction was carried out for 8hours.

The sample was removed and dried to a constant weight in an oven, cooled in a desiccator and reweighed and the percentage crude lipid content was determined thus;

$$\%\ lipid\ = \frac{Weight\ of\ lipid\ extracted}{Weight\ of\ dry\ sample} \times 100$$

Where the weight of lipid extracted was the loss in weight of the sample after extraction, drying in an oven and cooling in a desiccator.

4. Determination of crude fibre

Crude fibre was determined by the method in AOAC (1990). Two grams of grounded sample was placed in a round bottom flask. 100ml of 0.25M H_2SO_4 was added and mixture was boiled under reflux for 30 minutes. The insoluble matter was washed several times with hot water until it was acid free (C1). It was then transferred into a flask containing 100ml of 0.25M NaOH solution. The mixture was boiled again under reflux for 30 minutes and filtered under suction. The insoluble residue was washed with hot water until it is base free (C2). It was then ashed in a furnace at 550^oC for 2

hours. The furnace was then put off and allowed to cool down. The sample was then removed and cooled in a desiccator and weighed (C3). The crude fibre content was then calculated as loss of weight in ashing. Weight of original sample was used as W.

$$\%\ crude\ fiber\ = \frac{C2 - C3}{W} \times 100$$

5. Determination of nitrogen content and crude protein

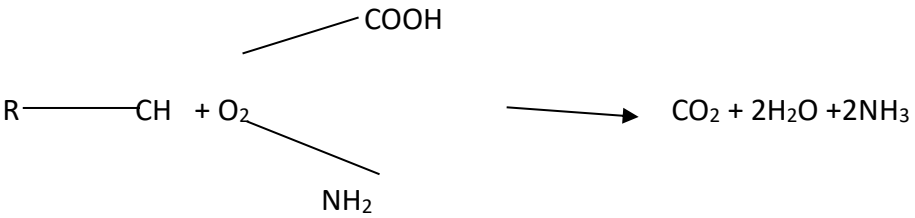
Principle

Proteins are major compounds containing nitrogen primarily in the form of amino acids which are their building blocks. Nitrogen is used as an index termed crude protein as distinct from true protein. The Kjedahl method in AOAC (1990) was used for the crude protein determination.

Steps for determination

A. mineralization steps of organic substance in boiling sulphuric acid.

$2H_2SO_4 \longrightarrow 2SO_2 + 2H_2O + O_2$



B. Distillation Steps of Ammonium Sulphate after Alkalisation of The Boric Acid Solution

$(NH_4)_2SO_4 + NaOH \longrightarrow 2Na_2SO_4 + 2H_2O + 2NH_3$

$NH_3 + H_2O \longrightarrow NH4OH$

$H_3BO_3 + NH_4OH \longrightarrow (NH_4)_3BO_3 + 3H_2O$

C. Titration of ammonium with hydrochloric acid of standardize concentration

$(NH_4)_3BO_3 + HCl \longrightarrow 3NH_4Cl + H_3BO_3$

Method

Exactly 2.0g of each sample was weighed into 100ml Kjedahl flask and a few anti bumping granules were added. One gram of the mixed catalyst ($CuSO_4$ and K_2SO_4 in the ratio 8:1 respectively) and 15ml of concentrated sulphuric acid were added. The flask was placed on a Kjedahl digestion rack and heated until a clear solution was obtained. At the end of the digestion, the flask was cooled and the sample was quantitatively transferred to a 100ml volumetric flask and made up to the mark with distilled water. Ten millilitres of the digest was transferred into Markham semi micro nitrogen steel tube, 10ml of 40% NaOH solution was then added cautiously. The sample was then steam distilled liberating ammonia into a 100ml conical flask containing 10ml of 4% boric acid and a drop of methyl blue indicator until the colour changed from pink to green. Exactly 30ml of sample volume was then collected. The content of the conical flask was then titrated with 0.1M HCl. The end point was indicated by a colour change from green to pink and the volume (v) of the acid for each distillate was noted. Percentage nitrogen per sample was calculated using the expression below

$$\%nitrogen = \frac{M \times v \times 14 \times 100}{Weight\ of\ sample \times 1000 \times 10} \times 100$$

Where, M = Molarity of HCl

14 = Atomic weight of nitrogen.

100 = Total volume of digest.

100 = % conversion.

10 = Volume of the digest taken.

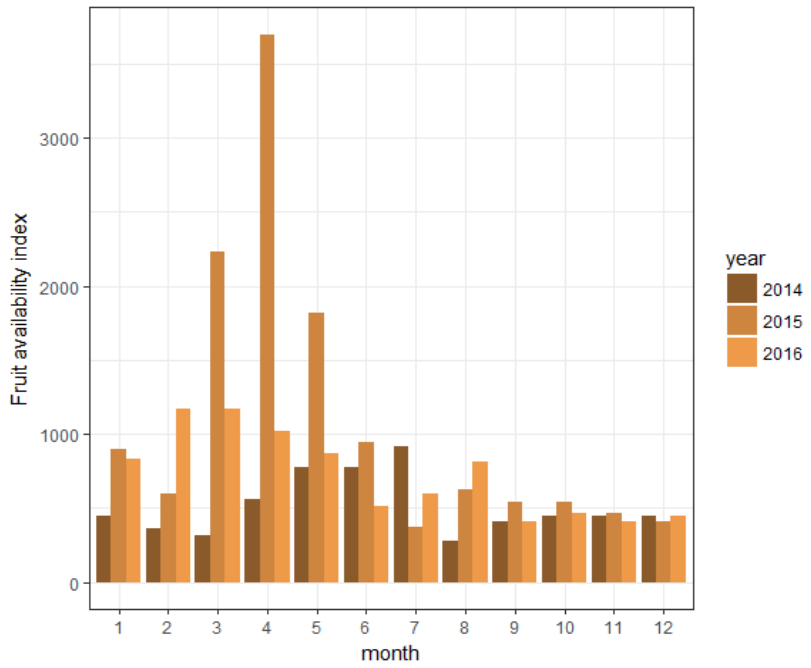
1000 = Conversion to litre.

The crude protein was calculateed as % Protein = 6.25 x % nitrogen.

6. Determination of carbohydrate content

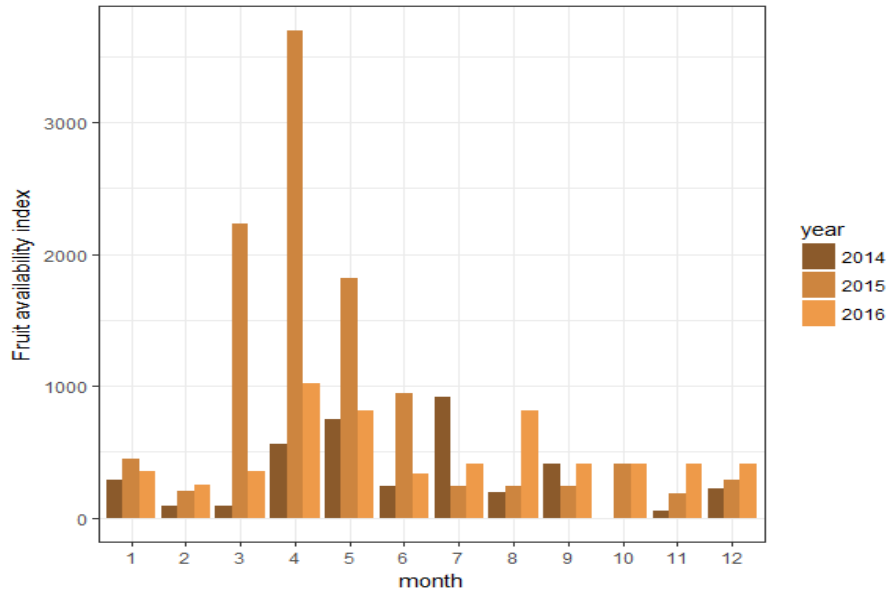
The percentage carbohydrate was obtained by difference thus;

Percentage carbohydrate = 100 - (%ash+%crude fibre+%crude fat+%moisture+%crude protein).



Appendix 5. 2.1: Figure showing the monthly fruit abundance indices of matured/ripe fruits in NNFR

2b.



Appendix 5.2.2: Figure showing the monthly fruit abundance indices of large-seeded species with matured/ripe fruits in NNFR

Appendix 5. 3: Table showing the output results of Bayesian model for posterior probabilities of seed predation in different species. External effects are highlighted and significant effects (i.e. confidence intervals consistently lower or higher than 0) are shown in bold.

Parameters	Mean	Standard error(mean)	Standard Deviation	Lcl (2.5%)	Lcl (25%)	Median (50%)	Ucl (75%)	Ucl (97.5)	n_eff	Rhat
Anthonotha:2014:E	-0.08	0.06	0.53	-1.18	-0.34	-0.05	0.24	0.81	93	1.04
Beilschmedia:2014:E	-1.5	0.05	0.53	-2.59	-1.76	-1.46	-1.2	-0.55	93	1.04
Carapa:2014:E	2.27	0.06	0.5	1.16	2.04	2.29	2.55	3.11	82	1.05
Santiria:2014:E	1.68	0.06	0.51	0.63	1.44	1.71	1.98	2.53	85	1.04
Anthonotha:2015:E	0.18	0.05	0.49	-0.86	-0.05	0.19	0.46	1	82	1.05
Beilschmedia:2015:E	-0.29	0.05	0.5	-1.33	-0.55	-0.26	-0.01	0.59	86	1.04
Carapa:2015:E	1.2	0.05	0.51	0.11	0.96	1.25	1.5	2.05	90	1.04
Anthonotha:2014:FC	0.71	0.05	0.52	-0.42	0.46	0.73	1.01	1.64	103	1.04
Beilschmedia:2014:FC	0.02	0.05	0.53	-1.15	-0.25	0.04	0.33	1	104	1.04
Carapa:2014:FC	2.54	0.05	0.5	1.47	2.3	2.56	2.82	3.45	92	1.04
Santiria:2014:FC	1.11	0.05	0.48	0.09	0.9	1.14	1.36	1.99	91	1.04
Anthonotha:2015:FC	0.44	0.05	0.49	-0.65	0.22	0.46	0.7	1.38	87	1.04
Beilschmedia:2015:FC	-0.32	0.05	0.5	-1.36	-0.56	-0.31	-0.05	0.57	97	1.04
Carapa:2015:FC	1.05	0.05	0.5	0.03	0.81	1.07	1.32	1.94	82	1.05
Anthonotha:2014:I	0.8	0.05	0.53	-0.29	0.53	0.82	1.11	1.78	98	1.04
Beilschmedia:2014:I	-0.81	0.05	0.55	-1.89	-1.1	-0.79	-0.49	0.15	118	1.03
Carapa:2014:I	2.19	0.05	0.49	1.18	1.95	2.21	2.47	3.1	91	1.04
Santiria:2014:I	1.72	0.05	0.5	0.66	1.48	1.74	1.99	2.63	88	1.04
Anthonotha:2015:I	0.66	0.05	0.49	-0.32	0.43	0.67	0.92	1.51	87	1.04
Beilschmedia:2015:I	-0.44	0.05	0.5	-1.41	-0.67	-0.42	-0.16	0.44	89	1.04
Carapa:2015:I	1.51	0.05	0.5	0.42	1.27	1.52	1.8	2.4	91	1.04
Litter cover	0.01	0	0.09	-0.15	-0.05	0.01	0.07	0.18	621	1
Distance to nearest water	-0.01	0	0.11	-0.22	-0.09	-0.01	0.06	0.21	621	1.01
Dead logs	-0.05	0	0.07	-0.18	-0.1	-0.05	0	0.1	922	1
Fruit abundance	**-0.31**	**0**	**0.06**	**-0.42**	**-0.34**	**-0.31**	**-0.27**	**-0.19**	**2000**	**1**
Herb cover	-0.05	0	0.09	-0.21	-0.11	-0.05	0.01	0.12	684	1

Appendix 5. 4: Table showing the output results of Bayesian model for posterior probabilities of seed caching in different species. External effects are highlighted and significant effects (i.e. confidence intervals consistently lower or higher than 0) are shown in bold.

Parameters	Mean	Standard error(mean)	Standard Deviation	Lcl (2.5%)	Lcl (25%)	Median (50%)	Ucl (75%)	Ucl (97.5)	n_eff	Rhat
Anthonotha:2014:E	-0.94	0.01	0.36	-1.65	-1.16	-0.94	-0.7	-0.24	989	1
Beilschmedia:2014:E	-4.94	0.02	0.85	-6.86	-5.42	-4.86	-4.34	-3.51	2000	1
Carapa:2014:E	-3.69	0.01	0.33	-4.38	-3.89	-3.67	-3.47	-3.09	916	1
Santiria:2014:E	-3.18	0.01	0.35	-3.88	-3.41	-3.17	-2.94	-2.54	934	1
Anthonotha:2015:E	-2.52	0.01	0.33	-3.17	-2.73	-2.51	-2.3	-1.89	904	1
Beilschmedia:2015:E	-3.5E+07	-3.1E+5	-6.0E+6	1.9E+08	-2.4E+07	-9571025	-514678	-31162.7	4	2.84
Carapa:2015:E	-2.9	0.01	0.34	-3.58	-3.12	-2.9	-2.68	-2.27	873	1
Anthonotha:2014:FC	-2.14	0.01	0.4	-2.94	-2.4	-2.13	-1.88	-1.37	1113	1
Beilschmedia:2014:FC	-3.42	0.01	0.55	-4.54	-3.78	-3.4	-3.04	-2.41	2000	1
Carapa:2014:FC	-4.77	0.01	0.49	-5.75	-5.08	-4.75	-4.44	-3.9	1203	1
Santiria:2014:FC	-2.7	0.01	0.33	-3.35	-2.9	-2.7	-2.5	-2.06	1021	1
Anthonotha:2015:FC	-1.61	0.01	0.31	-2.22	-1.81	-1.61	-1.42	-0.99	885	1
Beilschmedia:2015:FC	-6.26	0.04	1.34	-9.42	-7	-6.01	-5.29	-4.33	1075	1
Carapa:2015:FC	-3.39	0.01	0.38	-4.19	-3.62	-3.38	-3.14	-2.67	1102	1
Anthonotha:2014:I	-2.6	0.01	0.46	-3.48	-2.9	-2.6	-2.29	-1.73	2000	1
Beilschmedia:2014:I	-1.98	0.01	0.41	-2.81	-2.24	-1.98	-1.7	-1.17	1431	1
Carapa:2014:I	-3.87	0.01	0.35	-4.6	-4.08	-3.86	-3.66	-3.23	1144	1
Santiria:2014:I	-3.88	0.01	0.43	-4.76	-4.16	-3.85	-3.58	-3.1	1308	1
Anthonotha:2015:I	-1.91	0.01	0.3	-2.51	-2.09	-1.91	-1.73	-1.35	899	1
Beilschmedia:2015:I	-1.1E+07	-1.1E+06	-2.2E+06	-7.6E+07	-9.7E+06	-1.8E+06	-356622	-15989.5	4	1.41
Carapa:2015:I	-2.99	0.01	0.32	-3.64	-3.19	-2.97	-2.78	-2.38	1020	1
Litter cover	0.22	0	0.11	-0.01	0.14	0.22	0.3	0.44	1330	1
Distance to nearest water	0.21	0	0.14	-0.07	0.12	0.21	0.3	0.48	907	1
Dead logs	**0.18**	**0**	**0.1**	**0**	**0.12**	**0.18**	**0.25**	**0.37**	**925**	1.01
Fruit abundance	**-0.29**	**0**	**0.1**	**-0.48**	**-0.35**	**-0.28**	**-0.22**	**-0.1**	**2000**	**1**
Herb cover	**-0.25**	**0**	**0.11**	**-0.46**	**-0.32**	**-0.25**	**-0.18**	**-0.03**	**974**	**1**

Appendix 5. 5: Table showing the output results of Bayesian model for posterior probabilities of seed predation in different fat content levels. External effects are highlighted and significant effects (i.e. confidence intervals consistently lower or higher than 0) are shown in bold.

Parameters	**Mean**	**Standard error(mean)**	**Standard Deviation**	**Lcl (2.5%)**	**Lcl (25%)**	**Median (50%)**	**Ucl (75%)**	**Ucl (97.5)**	**n_eff**	**Rhat**
high:2014:E	2.43	0.03	0.45	1.61	2.16	2.39	2.67	3.46	274	1
low:2014:E	-0.66	0.03	0.45	-1.49	-0.92	-0.7	-0.43	0.32	284	1.01
moderate:2014:E	1.75	0.03	0.45	0.91	1.49	1.72	1.99	2.75	281	1
high:2015:E	1.4	0.03	0.45	0.57	1.14	1.37	1.64	2.39	280	1.01
low:2015:E	-0.08	0.03	0.43	-0.88	-0.34	-0.12	0.14	0.87	269	1
high:2014:FC	2.69	0.03	0.46	1.84	2.41	2.67	2.93	3.68	280	1.01
low:2014:FC	0.55	0.03	0.46	-0.33	0.26	0.54	0.81	1.47	275	1.01
moderate:2014:FC	1.18	0.03	0.45	0.3	0.92	1.16	1.42	2.17	270	1.01
high:2015:FC	1.22	0.03	0.46	0.32	0.95	1.19	1.45	2.2	277	1.01
low:2015:FC	0.07	0.03	0.44	-0.8	-0.18	0.05	0.29	1.01	267	1
high:2014:I	2.35	0.03	0.44	1.49	2.1	2.33	2.58	3.33	269	1.01
low:2014:I	0.34	0.03	0.45	-0.5	0.06	0.31	0.59	1.3	290	1.01
moderate:2014:I	1.81	0.03	0.45	0.98	1.54	1.78	2.03	2.83	279	1.01
high:2015:I	1.7	0.03	0.45	0.84	1.44	1.68	1.93	2.69	277	1
low:2015:I	0.21	0.03	0.43	-0.65	-0.05	0.18	0.42	1.17	262	1
Litter cover	0.01	0	0.09	-0.16	-0.05	0	0.06	0.18	888	1
Distance to nearest water	-0.03	0	0.11	-0.25	-0.1	-0.03	0.04	0.18	828	1.01
Dead logs	-0.04	0	0.07	-0.18	-0.09	-0.04	0.01	0.11	908	1
Fruit abundance	-0.07	0	0.03	-0.14	-0.09	-0.07	-0.05	0	2000	1
Herb cover	-0.05	0	0.08	-0.2	-0.1	-0.05	0.01	0.12	806	1

Appendix 5. 6: Table showing the output results of Bayesian model for posterior probabilities of seed caching in different fat content levels. External effects are highlighted and significant effects (i.e. confidence intervals consistently lower or higher than 0) are shown in bold.

Parameters	Mean	Standard error(mean)	Standard Deviation	Lcl (2.5%)	Lcl (25%)	Median (50%)	Ucl (75%)	Ucl (97.5)	n_eff	Rhat
high:2014:E	-3.4	0.02	0.37	-4.19	-3.63	-3.39	-3.15	-2.72	410	1.01
low:2014:E	-1.79	0.02	0.37	-2.54	-2.02	-1.78	-1.55	-1.05	295	1.01
moderate:2014:E	-3.18	0.02	0.39	-4.03	-3.43	-3.16	-2.92	-2.43	387	1.01
high:2015:E	-2.58	0.02	0.38	-3.39	-2.82	-2.57	-2.33	-1.86	428	1.01
low:2015:E	-3.68	0.02	0.36	-4.46	-3.92	-3.66	-3.44	-3.02	355	1.01
high:2014:FC	-4.47	0.02	0.49	-5.47	-4.81	-4.46	-4.14	-3.56	586	1
low:2014:FC	-2.24	0.02	0.41	-3.08	-2.49	-2.24	-1.97	-1.48	484	1
moderate:2014:FC	-2.66	0.02	0.38	-3.44	-2.91	-2.67	-2.41	-1.92	425	1.01
high:2015:FC	-3.05	0.02	0.41	-3.88	-3.31	-3.04	-2.79	-2.25	548	1
low:2015:FC	-2.73	0.02	0.33	-3.4	-2.93	-2.72	-2.51	-2.1	377	1.01
high:2014:I	-3.58	0.02	0.38	-4.34	-3.82	-3.57	-3.33	-2.86	502	1
low:2014:I	-1.89	0.02	0.39	-2.68	-2.16	-1.89	-1.64	-1.17	538	1
moderate:2014:I	-3.79	0.02	0.45	-4.71	-4.08	-3.77	-3.47	-2.98	654	1
high:2015:I	-2.64	0.02	0.37	-3.43	-2.89	-2.64	-2.39	-1.94	539	1
low:2015:I	-3.02	0.02	0.32	-3.7	-3.22	-3.02	-2.82	-2.42	452	1
Litter cover	0.21	0	0.12	-0.03	0.13	0.2	0.29	0.45	986	1.01
Distance to nearest water	0.21	0.01	0.14	-0.08	0.12	0.21	0.31	0.49	650	1.01
Dead logs	**0.21**	**0**	**0.1**	**0.01**	**0.15**	**0.21**	**0.28**	**0.42**	**844**	**1.01**
Fruit abundance	**0.35**	**0**	**0.07**	**0.22**	**0.3**	**0.35**	**0.39**	**0.48**	**2000**	**1**
Herb cover	**-0.23**	**0**	**0.12**	**-0.47**	**-0.31**	**-0.23**	**-0.15**	**-0.02**	**988**	**1**

Appendix 5. 7: Table showing the output results of Bayesian model for posterior probabilities of seed predation in different protein content levels. External effects are highlighted and significant effects (i.e. confidence intervals consistently lower or higher than 0) are shown in bold.

Parameters	Mean	Standard error(mean)	Standard Deviation	Lcl (2.5%)	Lcl (25%)	Median (50%)	Ucl (75%)	Ucl (97.5)	n_eff	Rhat
high:2014:E	1.65	0.02	0.38	0.82	1.43	1.67	1.88	2.37	269	1.01
low:2014:E	1.07	0.02	0.36	0.28	0.88	1.09	1.29	1.74	240	1.01
low:2015:E	0.34	0.02	0.36	-0.49	0.15	0.36	0.55	1.02	232	1.01
high:2014:FC	1.09	0.02	0.38	0.26	0.87	1.1	1.31	1.81	292	1.01
low:2014:FC	1.78	0.02	0.36	0.96	1.59	1.8	2	2.45	288	1.01
low:2015:FC	0.43	0.02	0.36	-0.38	0.24	0.46	0.64	1.09	278	1.01
high:2014:I	1.71	0.02	0.4	0.88	1.48	1.72	1.96	2.47	281	1.01
low:2014:I	1.56	0.02	0.37	0.72	1.36	1.57	1.78	2.25	271	1.01
low:2015:I	0.6	0.02	0.36	-0.21	0.4	0.62	0.8	1.28	250	1.01
Litter cover	0	0	0.08	-0.17	-0.05	0	0.06	0.16	1058	1
Distance to nearest water	-0.02	0	0.1	-0.22	-0.09	-0.02	0.04	0.17	1025	1
Dead logs	-0.03	0	0.07	-0.17	-0.07	-0.02	0.02	0.11	1112	1
Fruit abundance	**-0.28**	**0**	**0.03**	**-0.34**	**-0.3**	**-0.28**	**-0.26**	**-0.22**	**2000**	**1**
Herb cover	-0.04	0	0.08	-0.2	-0.1	-0.04	0.01	0.12	1188	1

Appendix 5. 8: Table showing the output results of Bayesian model for posterior probabilities of seed caching in different protein content levels. External effects are highlighted and significant effects (i.e. confidence intervals consistently lower or higher than 0) are shown in bold.

Parameters	Mean	Standard error(mean)	Standard Deviation	Lcl (2.5%)	Lcl (25%)	Median (50%)	Ucl (75%)	Ucl (97.5)	n_eff	Rhat
high:2014:E	-3.12	0.01	0.35	-3.82	-3.33	-3.11	-2.91	-2.49	725	1.01
low:2014:E	-2.79	0.01	0.29	-3.35	-2.96	-2.79	-2.62	-2.25	514	1.01
low:2015:E	-3.25	0.01	0.29	-3.82	-3.42	-3.24	-3.07	-2.72	516	1.01
high:2014:FC	-2.66	0.02	0.35	-3.36	-2.87	-2.66	-2.43	-1.98	502	1
low:2014:FC	-3.45	0.02	0.33	-4.04	-3.65	-3.45	-3.25	-2.8	432	1
low:2015:FC	-2.71	0.01	0.29	-3.23	-2.89	-2.71	-2.55	-2.15	389	1
high:2014:I	-3.77	0.01	0.42	-4.58	-4.04	-3.76	-3.49	-2.97	1072	1
low:2014:I	-3.05	0.01	0.29	-3.55	-3.22	-3.05	-2.87	-2.48	520	1.01
low:2015:I	-2.85	0.01	0.27	-3.34	-3.01	-2.85	-2.7	-2.34	539	1
Litter cover	0.22	0	0.12	-0.01	0.15	0.22	0.3	0.47	984	1
Distance to nearest water	0.18	0.01	0.14	-0.08	0.09	0.18	0.28	0.47	232	1.02
Dead logs	0.19	0	0.1	0	0.12	0.19	0.26	0.39	815	1
Fruit abundance	**0.27**	**0**	**0.05**	**0.16**	**0.23**	**0.27**	**0.3**	**0.37**	**2000**	**1**
Herb cover	**-0.24**	**0**	**0.11**	**-0.46**	**-0.31**	**-0.23**	**-0.16**	**-0.04**	**747**	**1.01**

Appendix 5. 9: Table showing the output results of Bayesian model for posterior probabilities of seed predation in different fibre content levels. External effects are highlighted and significant effects (i.e. confidence intervals consistently lower or higher than 0) are shown in bold.

Parameters	**Mean**	**Standard error(mean)**	**Standard Deviation**	**Lcl (2.5%)**	**Lcl (25%)**	**Median (50%)**	**Ucl (75%)**	**Ucl (97.5)**	**n_eff**	**Rhat**
high:2014:E	-0.7	0.03	0.45	-1.62	-0.94	-0.68	-0.44	0.17	260	1.01
low:2014:E	2.4	0.03	0.45	1.46	2.17	2.41	2.66	3.26	261	1.01
moderate:2014:E	1.72	0.03	0.44	0.81	1.48	1.73	1.97	2.62	256	1.01
high:2015:E	-0.12	0.03	0.42	-1.03	-0.34	-0.11	0.11	0.71	243	1.01
low:2015:E	1.37	0.03	0.44	0.5	1.14	1.37	1.62	2.23	250	1.01
high:2014:FC	0.51	0.03	0.44	-0.37	0.27	0.52	0.74	1.4	262	1.01
low:2014:FC	2.65	0.03	0.45	1.79	2.41	2.67	2.9	3.55	264	1.01
moderate:2014:FC	1.14	0.03	0.44	0.25	0.9	1.15	1.38	2	251	1.01
high:2015:FC	0.02	0.03	0.43	-0.86	-0.19	0.03	0.25	0.92	247	1.01
low:2015:FC	1.17	0.03	0.44	0.31	0.94	1.18	1.42	2.05	250	1.01
high:2014:I	0.28	0.03	0.45	-0.6	0.04	0.27	0.54	1.17	270	1.01
low:2014:I	2.3	0.03	0.45	1.45	2.05	2.32	2.55	3.23	280	1.01
moderate:2014:I	1.75	0.03	0.44	0.88	1.5	1.76	2	2.63	295	1.01
high:2015:I	0.16	0.03	0.42	-0.65	-0.07	0.16	0.37	1	260	1.01
low:2015:I	1.65	0.03	0.45	0.76	1.4	1.65	1.91	2.52	280	1.01
Litter cover	0	0	0.08	-0.16	-0.05	0	0.06	0.17	675	1
Distance to nearest water	-0.03	0	0.1	-0.23	-0.1	-0.03	0.04	0.17	596	1.01
Dead logs	-0.04	0	0.08	-0.19	-0.09	-0.04	0.01	0.11	874	1
Fruit abundance	-0.07	0	0.04	-0.14	-0.09	-0.07	-0.05	0	2000	1
Herb cover	-0.05	0	0.09	-0.21	-0.1	-0.05	0.01	0.12	905	1

Appendix 5. 10: Table showing the output results of Bayesian model for posterior probabilities of seed caching in different fibre content levels. External effects are highlighted and significant effects (i.e. confidence intervals consistently lower or higher than 0) are shown in bold.

Parameters	Mean	Standard error(mean)	Standard Deviation	Lcl (2.5%)	Lcl (25%)	Median (50%)	Ucl (75%)	Ucl (97.5)	n_eff	Rhat
high:2014:E	-1.8	0.03	0.45	-2.54	-2.06	-1.8	-1.55	-0.93	258	1.02
low:2014:E	-3.42	0.03	0.44	-4.18	-3.68	-3.41	-3.18	-2.58	269	1.02
moderate:2014:E	-3.2	0.03	0.46	-4.02	-3.47	-3.2	-2.93	-2.33	301	1.01
high:2015:E	-3.69	0.03	0.45	-4.52	-3.93	-3.68	-3.45	-2.9	254	1.02
low:2015:E	-2.6	0.03	0.45	-3.38	-2.84	-2.6	-2.35	-1.76	271	1.02
low:2013:FC	-3.11	0.03	0.58	-4.25	-3.47	-3.1	-2.75	-2	429	1.01
high:2014:FC	-2.25	0.03	0.48	-3.12	-2.52	-2.26	-1.99	-1.34	292	1.02
low:2014:FC	-4.49	0.03	0.55	-5.55	-4.82	-4.47	-4.15	-3.47	370	1.02
moderate:2014:FC	-2.67	0.03	0.45	-3.5	-2.92	-2.67	-2.42	-1.79	258	1.03
high:2015:FC	-2.73	0.03	0.43	-3.44	-2.97	-2.74	-2.51	-1.87	238	1.02
low:2015:FC	-3.05	0.03	0.49	-3.91	-3.35	-3.07	-2.76	-2.07	295	1.02
high:2014:I	-1.91	0.03	0.46	-2.68	-2.19	-1.92	-1.65	-0.97	262	1.02
low:2014:I	-3.59	0.03	0.46	-4.41	-3.85	-3.6	-3.33	-2.75	283	1.02
moderate:2014:I	-3.8	0.03	0.53	-4.79	-4.12	-3.8	-3.48	-2.83	309	1.02
high:2015:I	-3.03	0.03	0.42	-3.72	-3.26	-3.04	-2.83	-2.25	231	1.02
low:2015:I	-2.66	0.03	0.45	-3.46	-2.93	-2.66	-2.4	-1.84	264	1.02
Litter cover	**0.2**	**0**	**0.12**	**-0.04**	**0.12**	**0.2**	**0.28**	**0.45**	**867**	**1**
Distance to nearest water	**0.22**	**0.01**	**0.14**	**-0.06**	**0.12**	**0.22**	**0.31**	**0.53**	**740**	**1**
Dead logs	**0.22**	**0**	**0.1**	**0.02**	**0.15**	**0.22**	**0.28**	**0.42**	**804**	**1**
Fruit abundance	**0.35**	**0**	**0.07**	**0.22**	**0.31**	**0.35**	**0.4**	**0.48**	**2000**	**1**
Herb cover	**-0.23**	**0**	**0.11**	**-0.46**	**-0.3**	**-0.23**	**-0.15**	**-0.01**	**936**	**1**

Appendix 5. 11: Table showing the output results of Bayesian model for posterior probabilities of seed predation in different carbohydrate content levels. External effects are highlighted and significant effects (i.e. confidence intervals consistently lower or higher than 0) are shown in bold.

Parameters	Mean	Standard error(mean)	Standard Deviation	Lcl (2.5%)	Lcl (25%)	Median (50%)	Ucl (75%)	Ucl (97.5)	n_eff	Rhat
high:2014:E	2.15	0.02	0.38	1.44	1.94	2.15	2.36	2.84	389	1
moderate:2014:E	-0.69	0.02	0.39	-1.44	-0.91	-0.68	-0.45	0.03	427	1
high:2015:E	1.38	0.02	0.39	0.61	1.16	1.38	1.61	2.1	422	1
moderate:2015:E	-0.07	0.02	0.37	-0.8	-0.28	-0.06	0.13	0.63	392	1
high:2014:FC	1.99	0.02	0.38	1.32	1.77	1.97	2.19	2.71	411	1
moderate:2014:FC	0.52	0.02	0.39	-0.22	0.3	0.51	0.75	1.26	458	1
high:2015:FC	1.19	0.02	0.39	0.5	0.95	1.18	1.41	1.93	426	1
moderate:2015:FC	0.08	0.02	0.37	-0.59	-0.12	0.07	0.29	0.79	401	1
high:2014:I	2.11	0.02	0.37	1.42	1.9	2.1	2.3	2.82	402	1
moderate:2014:I	0.3	0.02	0.38	-0.4	0.06	0.28	0.52	1.04	425	1
high:2015:I	1.66	0.02	0.39	0.92	1.43	1.65	1.87	2.43	435	1
moderate:2015:I	0.21	0.02	0.36	-0.48	0	0.19	0.4	0.89	396	1
Litter cover	0.01	0	0.09	-0.16	-0.05	0.01	0.07	0.17	696	1.01
Distance to nearest water	-0.03	0	0.11	-0.24	-0.1	-0.03	0.04	0.17	694	1
Dead logs	-0.04	0	0.08	-0.19	-0.09	-0.04	0.01	0.11	697	1.01
Fruit abundance	**-0.1**	**0**	**0.03**	**-0.16**	**-0.12**	**-0.1**	**-0.07**	**-0.04**	**2000**	**1**
Herb cover	-0.05	0	0.08	-0.21	-0.1	-0.05	0.01	0.11	846	1

Appendix 5. 12: Table showing the output results of Bayesian model for posterior probabilities of seed caching in different carbohydrate content levels. External effects are highlighted and significant effects (i.e. confidence intervals consistently lower or higher than 0) are shown in bold

Parameters	Mean	Standard error(mean)	Standard Deviation	Lcl (2.5%)	Lcl (25%)	Median (50%)	Ucl (75%)	Ucl (97.5)	n_eff	Rhat
high:2014:E	-3.32	0.01	0.36	-4.08	-3.54	-3.32	-3.11	-2.63	789	1
moderate:2014:E	-1.79	0.01	0.38	-2.59	-2.02	-1.78	-1.55	-1.05	807	1
high:2015:E	-2.6	0.01	0.39	-3.38	-2.84	-2.6	-2.35	-1.85	841	1
moderate:2015:E	-3.72	0.01	0.37	-4.47	-3.95	-3.71	-3.48	-3.07	804	1
high:2014:FC	-3.45	0.01	0.38	-4.22	-3.69	-3.46	-3.23	-2.69	797	1
moderate:2014:FC	-2.23	0.02	0.43	-3.05	-2.51	-2.24	-1.98	-1.35	794	1
high:2015:FC	-3.04	0.01	0.44	-3.94	-3.32	-3.04	-2.75	-2.22	891	1
moderate:2015:FC	-2.75	0.01	0.35	-3.43	-2.98	-2.75	-2.54	-2.07	714	1
high:2014:I	-3.65	0.01	0.37	-4.36	-3.89	-3.64	-3.4	-2.94	744	1
moderate:2014:I	-1.9	0.01	0.4	-2.7	-2.16	-1.91	-1.65	-1.1	985	1
high:2015:I	-2.65	0.01	0.39	-3.41	-2.9	-2.65	-2.4	-1.85	881	1
moderate:2015:I	-3.06	0.01	0.35	-3.74	-3.29	-3.05	-2.85	-2.38	836	1
Litter cover	0.2	0	0.12	-0.04	0.12	0.2	0.28	0.45	1550	1
Distance to nearest water	0.22	0	0.15	-0.06	0.12	0.22	0.32	0.52	950	1
Dead logs	**0.22**	**0**	**0.1**	**0.02**	**0.15**	**0.22**	**0.28**	**0.42**	**2000**	**1**
Fruit abundance	**0.37**	**0**	**0.07**	**0.24**	**0.32**	**0.37**	**0.41**	**0.5**	**2000**	**1**
Herb cover	**-0.23**	**0**	**0.11**	**-0.46**	**-0.31**	**-0.23**	**-0.15**	**-0.01**	**1087**	**1**